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**Predator-prey relations and density estimation based on camera  
trap data in Bükk National Park, Hungary**

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# Abstract

Large carnivores are recovering in many regions of Europe, which generates many conflicts with different stakeholders. Bükk National Park in Hungary is a suitable area to study the effects of the natural return of the wolf (*Canis lupus*) on local wildlife. Wolf and ungulate densities, and the effect of wolf presence on its prey species, are often highlighted by local practitioners. One way to determine whether the wolf's prey, such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and a potential competitor, as the red fox (*Vulpes vulpes*), are adapted to the presence of the wolf, is to analyse the overlap of activity periods using camera trap data. In order to have reliable population densities, Random Encounter Model (REM) was used to estimate prey and predator population densities from camera trap data without individual recognition.

According to the study results, wolf has adapted its activity to the daily cycles of its main prey species, however at certain sensitive seasons of the year (e.g. rutting period or when young is born), wild boars and roe deer might use temporal segregation as a measure to avoid encounters with wolves. Wild boars showed the least overlap ( $\Delta=0.5$ ) at the time of gestation and when piglets are born. Second lowest overlap was between wolf and roe deer at rutting period ( $\Delta=0.64$ ), while interestingly, at its rutting period, red deer showed high overlap with wolves ( $\Delta=0.79$ ).

Camera trap-based population density estimations are similar to the National Park's STR marker-based genetic references from the area ( $STRn=14$  while  $REM\bar{n}=16$  individuals;  $\overline{SD}=1.28$  individuals), thus REM can be recommended to complement existing wildlife monitoring strategies in order to cross-check data from used methods (like visual observations, STR marker-based genetic analysis) and have a more reliable and cost-effective result in the end.

**Key-words:** *Canis lupus*, wild ungulates, activity range overlap, Random Encounter Model, camera-trap, Hungary

# Resumo

No presente, as populações de grandes carnívoros estão a recuperar em muitas regiões da Europa o que tem conduzido ao recrudescente dos conflitos com o homem. Os conflitos entre humanos e animais selvagens estão relacionados com a predação e em fortes preconceitos e crenças, e a resolução dos mesmos deve basear-se em dados científicos robustos. O Parque Nacional de Bükk, na Hungria, onde o lobo (*Canis lupus*) está a regressar por processos naturais, é uma área adequada para estudar os efeitos do retorno desta espécie nas populações locais de ungulados selvagens e mesocarnívoros. Investigar o efeito da presença do lobo nas suas presas naturais é um dos objetivos do parque nacional.

Para analisar se as presas do lobo, como o veado (*Cervus elaphus*), o corço (*Capreolus capreolus*), o javali (*Sus scrofa*) e a raposa (*Vulpes vulpes*), estão a responder à presença do predador, determinou-se a sobreposição dos períodos de atividade do predador versus o das presas. Complementarmente estimaram-se as densidades populacionais deste carnívoro e das suas presas silvestres, recorrendo a Modelos de Encontros Aleatórios (REM- Random Encounter Models). Em ambas as análises, utilizaram-se dados obtidos com recurso à armadilhagem fotográfica, sem reconhecimento individual.

De acordo com os resultados obtidos, o lobo adaptou a sua atividade aos ciclos diários da atividade das suas principais presas; no entanto, em certas estações do ano (por exemplo, o período de cio ou dos nascimentos), javalis e veados aparentam recorrer a uma segregação temporal para evitar encontros com os lobos. Os javalis mostraram a menor sobreposição ( $\Delta=0,5$ ) durante o período de gestação e nascimentos. A segunda menor sobreposição observada, foi entre o lobo e o corço no período de cio deste ( $\Delta=0,64$ ). No período do cio do veado, esta espécie apresentou uma elevada sobreposição de atividade com os lobos ( $\Delta=0,79$ ).

As estimativas das densidades populacionais das espécies em questão no Parque Nacional de Bükk, obtidas com a armadilhagem fotográfica, são semelhantes às obtidas por outros autores com recurso a marcadores genéticos de microssatélites (Short Tandem Repeat - STRn=14 enquanto  $REM\bar{n}=16$  indivíduos;  $SD=1,28$  indivíduos). Assim, sugerimos a utilização de modelos REM para complementar as estratégias de monitorização da vida selvagem existentes (observações diretas, análises genéticas) por forma a obterem-se resultados mais robustos.

**Palavras-chave:** *Canis lupus*, ungulados selvagens, sobreposição de faixa de atividade, Modelo de Encontro Aleatório, armadilha fotográfica, Hungria

# Chapter 1 - General introduction

Large carnivores play an essential role in the top-down regulation of natural ecosystems. Being on the top of the trophic pyramid, as apex predators, they can control the lower trophic levels and structure the ecosystem not only by limiting large herbivores through predation (Ripple and Beschta 2012), but also by altering their behaviour (Kuijper et al. 2013). The behavioural complex, when individuals optimize foraging efforts and safety under predation risk, is usually referred to as the ecology of fear (Brown et al. 1999). Prey can lower this risk in several ways: avoiding each other spatially (Kuijper et al. 2013) or temporally (Ross et al. 2013). It is also possible that the prey increases its vigilance level, as it was shown in the case of elk (*Cervus elaphus*) hinds in Wyoming (Childress and Lung 2003). Lowering movement rate and avoiding possible encounters with predators is another strategy, as it was shown in the case of hunting season survived elks and red deer (*Cervus elaphus*) that avoided open spaces, where the chance to encounter hunters was higher (Ciuti et al. 2012; Lone et al. 2015).

Another predator-avoidance strategy is temporal niche partitioning, with time being an ecological resource, thus equivalent to a niche axis (Schoener 1974). However, large carnivores can also have significant effects on other predators. Australia's keystone predator, the dingo (*Canis lupus dingo*) was proved to control the activity of problematic mesopredators, such as red fox (*Vulpes vulpes*) or feral cats (*Felis catus*) not only by direct predation but also by intraguild competition which contributes to the flourishing of local biodiversity (Claridge and Hunt 2008).

Carnivores ability to reduce prey densities and to affect other predators and to alter their behaviour can lead to multiple cascade effects contributing to the thrive of otherwise suppressed ecological or even geological processes. For example, wolf (*Canis lupus*) reintroduction in the Yellowstone National Park has triggered a trophic cascade by reducing elk (*Cervus elaphus*) populations and allowing riparian vegetation, especially willow (*Salix* spp.) to regenerate and thus provide material for beavers (*Castor fiber*) to build dams that after all changed the hydrological regime (Wolf et al. 2007). Trophic cascades are not always as visible or strong in their effects as it was shown in the above-mentioned studies.

Sometimes human activity can alter an ecosystem in a way where solely the reappearance of large carnivores cannot reverse the process of natural regeneration (Marshall et al. 2013).

All these three pillars of the role of large carnivores in the ecosystems, namely (i) predation, (ii) behaviour-changing potential and (iii) intraguild/intraspecific competition, could be studied. The level of direct consumption can be investigated by measuring the changes in the local prey species' population densities, while behavioural adaptations and intraguild competition could be measured through different prey behavioural characteristics.

In Europe, little is known, however, how prey would react when one of their most important predators returns. Re-appearance of large carnivores, like the wolf, Eurasian lynx (*Lynx lynx*), brown bear (*Ursus arctos*) and wolverines (*Gulo gulo*) all across Europe is a recent event that challenges society, wildlife managers and conservationists (Chapron et al. 2014).

To acquire data that allows to understand this complex system, reliable data on presence-absence, population trend or density, must be gathered. Trapping, catching or hunting large mammals, however, could be challenging and solicitous. These predators have low densities, large territories, are nocturnal and elusive (Hunter 2011; Bihari et al. 2006). Furthermore, many times they are threatened, which means capturing and handling the animal could put an extra threat on their fitness or survival. These traits make them hard to study with invasive methods which require the handling and many times penetrating the animal to get biological samples (Long et al. 2008).

The best option for monitoring large herbivores and carnivores are the so-called non-invasive methods. The common feature of these harmless techniques is that they do not disturb the natural behaviour of the animals. Camera traps, as a wide-range accepted non-invasive tool, can overcome many of the above mentioned problems (Wearn et al. 2017). Cameras provide consecutive information on long term and are relatively cheap which makes them more and more ubiquitous in wildlife management practice. So, new technologies and statistical approaches are keep emerging to solve formerly demanding conservation management challenges.

Within the scope of this thesis, camera trap data from Bükk National Park Directorate (Hungary), and two relatively new methods will be used to investigate behavioural adaptations of prey to the presence of the wolf:

a) Calculating the coefficient of overlap of the activity curves (Meredith and Ridout 2016) between the wolf and

(i) its common prey species such as red deer, roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), to see up to which level the behaviour of the prey species is affected by the presence of the wolf;

(ii) the most common mesocarnivore in the area, the red fox, to see if there is temporal segregation between ecologically similar species to avoid intraguild competition;

b) Random Encounter Model (REM) (Rowcliffe et al. 2008) to estimate wolf, wild boar, red and roe deer population density and compare the results with previous estimates based on harvest bag data (ungulates) and microsatellite-based DNA analysis (wolf).

Furthermore, recommendations will be given for future wildlife management practice based on the results of this thesis.

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# Chapter 2 - Prey-predator temporal overlap in Bükk National Park, Hungary

## Abstract

Returning wolves (*Canis lupus*) in Hungary create much tension between farmers and hunters who often complain that these animals disturb livestock and local wildlife and make hunting more complicated. Indeed, large carnivores by their position on the trophic pyramid as apex predators, have the potential to influence the behaviour and the numbers of their prey, as well as small carnivores.

In order to avoid energy loss by unsuccessful hunting, large carnivores are able to adapt their activity patterns with their most consumed prey, shifting their active periods during the day, on behalf of the herbivores.

Wolves are returning in the last decades to Bükk National Park, Hungary. The possible temporal segregation between functional groups (prey-predators) or at species level in certain periods of the year was studied by analysing camera trap data. Activity overlap analysis revealed a generally high overlap for functional groups ( $\Delta=0.77$ ; 95% CI [0.68-0.88]). Nevertheless, at species level, during some shorter periods, moderated overlaps was identified. These were the rutting period for the roe deer (*Capreolus capreolus*) ( $\Delta=0.64$ ; 95% CI [0.50-0.63]), and gestation and piglet-upbringing period for the wild boar (*Sus scrofa*) ( $\Delta=0.5$ ; 95% CI [0.35-0.73]). The wolf third most consumed prey in Hungary, the red deer (*Cervus elaphus*), showed an almost constant high overlap (lowest:  $\Delta=0.76$ ; 95% CI [0.64-0.85]); highest:  $\Delta=0.81$ ; 95% CI [0.72-0.92]). Fox (*Vulpes vulpes*) also had a generally high overlap with wolf ( $\Delta=0.83$ ; 95% CI [0.77-0.93]). Roe deer rutting period activity also indicated a slightly moderated regression compared to fox's activity ( $\Delta=0.74$ ; 95% CI [0.61-0.80]).

The results did not completely confirm hunters' observations, as the general high overlap rather indicates a stable co-existence between the wolf and wild ungulates, however at critical periods of the year herbivores might alter their behaviour to avoid encounters with the wolf.

# Introduction

Large carnivores are on the top of the trophic pyramid and by this position they have certain effects on lower trophic levels not only by direct predation (Ripple and Beschta 2012) but by altering the behaviour of their preys and other competitors (Kuijper et al. 2013; Ross et al. 2013; Wang et al. 2015). This behavioural complex, when individuals optimize foraging efforts and safety under predation risk, is often referred as the ecology of fear (Brown et al. 1999). Prey usually respond to predation risk with increasing its alertness, vigilance level (Laundré et al. 2001) or even its aggressiveness, as it was observed in Switzerland after the re-introduction of lynx (Breitenmoser and Haller 1993). The authors referred to this suddenly developed behavioural reaction of formerly naïve prey as behavioural depression, which develops after the detection of the presence of a formerly absent predator in the area. Temporal niche segregation from its predator could be one of these responses of prey species (Schoener 1974).

On the predators' side, however, it is known that access to vital resources, especially prey, play an important role in determining carnivores' daily activity cycles (Brown et al. 2001). In some cases carnivores adjusted their foraging period to align with the activity pattern of their most consumed prey in order to optimize energy gain and loss (Brown et al. 2001; Foster et al. 2013). Camera trap observations of jaguar (*Panthera onca*) revealed that no matter the species is considered mostly nocturnal across different habitats, in specific locations with high availability of diurnal prey, jaguars developed diurnal activity peaks (Foster et al. 2013).

This means, there is a constant competition between preys and their predators for maximizing foraging and reproduction gain while minimizing the risk of fatal encounters with predators or lethal energy loss by unsuccessful hunting (Lima and Dill 1990).

When sympatric carnivores are present, competition for valuable resources is inevitable – this is often referred as interspecific or intraguild competition (Hunter and Caro 2008). Bassi et al. (2012) found a low level trophic niche overlap (Pianka's  $O=0.356$ ) between wolf (*C. lupus*) and red fox (*V. vulpes*) in the Italian Appenines, that might be true in Hungary as well, where red fox also known to prey on young and small-sized ungulates (roe deer (*C. capreolus*) fawns or wild boar (*S. scrofa*) piglets) (Bassi et al. 2012; Patkó, pers. comm.). As large

carnivores has the potential to control smaller predators, by forcing them to change their behaviour, spatial or temporal use of the surrounding environment and resources (Hunter and Caro 2008; Johnson et al. 1996), temporal avoidance by the fox might be a manifestation of intraguild competition for valuable resources between the two species.

Wolf recolonisation is a recent event in Europe, that causes many conflicts between different stakeholder groups (e.g. livestock breeders, hunters, forestry or conservationists). Further elaborates the situation the fact that, for example in Hungary, where the species was not present for more than 50 years, many livestock breeders have already gave up using traditional protection measures - shepherd presence , fences or livestock guardian dogs. This led to unprotected herds and flocks, which are easy targets for wolves (Gula 2008; Højberg et al. 2017). Hunters also complain that the expanding wolf population not only predate, but simply by their presence, disturbs the normal behaviour of ungulates that makes hunting complicated (Højberg et al. 2017; Patkó, pers comm.).

In this study I am going to investigate whether there is any sign of disturbance in the activity of ungulate species or the fox by comparing their daily activity patterns to the wolves'. I am going to investigate if the sign of disturbance is constant through the life cycle or if there are more sensible seasons when animals avoid each other, for example when there are fragile newborns in the population or when resources overlap (in the case of the fox) - or the opposite: take less care, for example when it is more to loose by missing a chance for reproduction than by avoiding encounters with predators (Laundré et al. 2001).

For this purpose, I am going to use camera trap data collected by the Bükk National Park Directorate, which is one of the foci of the Hungarian wolf populations. Camera traps are excellent measures for long-term behavioural observations as they are relatively cheap, they do not disturb the normal activity and behaviour of animals and they can provide information even of elusive or rare species (Griffiths and van Schaik 1993). As footages record the date and the time, they can be used for investigating daily activity patterns of a species, also their change through time (e.g. seasons, years). Activity patterns compared between different species may result in indicating signs of competition or predation (Azevedo et al. 2018, Foster et al. 2013, Ridout and Linkie 2009).

My hypothesis is that if hunters' observations are valid, then ungulates' daily activity will be different than of wolves' in order to reduce the chance of encounters. I, however, assume that there will be no general difference between the daily activity of wolves and its 3 potential prey species: roe deer, red deer (*C. elaphus*) and wild boars, because carnivores tend to adapt to the daily activity rhythm of their main prey, making them coexist with each other at the same time and location. Wolf has never been completely eradicated (Gombkötő, pers. comm.) from the area thus they had enough time to synchronize their activity with their prey.

## Materials and Methods

### Study area

The study area is located (**Fig. 2**) in the Bükk National Park on the north-eastern part of Hungary with the area of 42 296 ha (390.63 km<sup>2</sup>). Although the highest points of Bükk Mountains are still below 1000 m (highest peak is Istállóskő with 959 m), there are more than 50 which are above 900 m and 11 out of these are between 950-959 m, thus it is considered as a high elevation habitat in Hungary.

The vegetation is dominated by forest (94%) of native tree species of European beech (*Fagus sylvatica*) (35%), Sessile oak (*Quercus petraea*) (32%), European hornbeam (*Carpinus betulus*) (13%) and Turkey oak (*Quercus cerris*) (7%) (Baráz 2002). (**Fig. 1**)



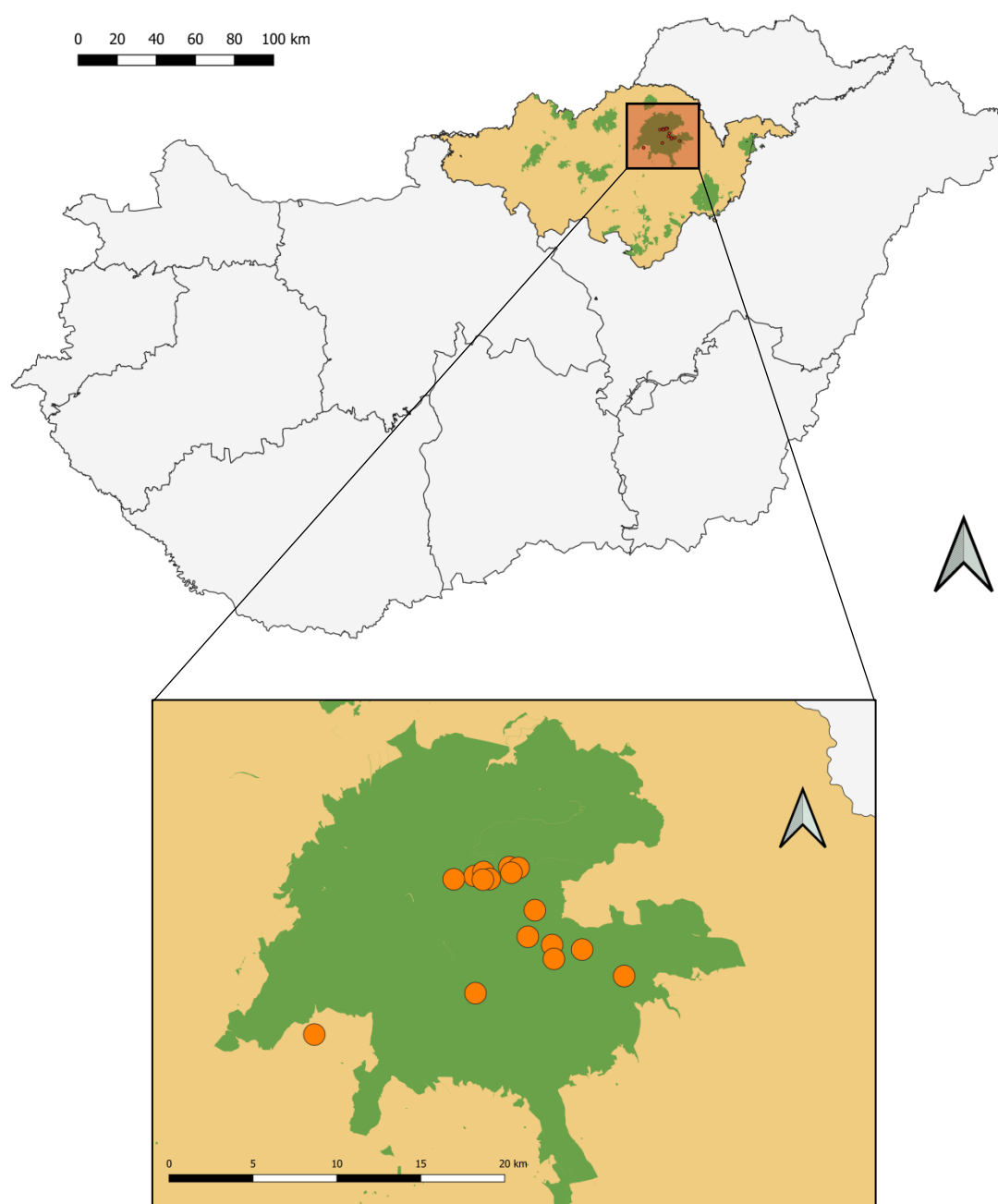
**Fig. 1.** Landscape view of the Bükk Mountains (Photo credit: Zsolt Halasi).

Due to a significant continental influence, the winter is cold (average January temperature is  $-4\text{ }^{\circ}\text{C}$ ) and snowy days are the most in the country. Summer is warm, thunderstorms are common in the beginning of July-end of August which cause two precipitation maximum in the area and the total annual precipitation of 773 mm. Despite the relatively high amount of precipitation, the Bükk Mountains are poor in rivers or still water bodies. The average annual temperature is approximately  $2\text{ }^{\circ}\text{C}$  lower than the national average, which equals to  $7\text{--}8\text{ }^{\circ}\text{C}$  degree here.

According to the fauna, the Bükk National Park and the surrounding areas are richer in vertebrates than national average and many of them are protected in Hungary with several Carpathian species. According to the Bükk National Park Directorate one of the major conservation issues in the area is the high density of large herbivore population – returning large carnivores, like the wolf or the lynx, could play an important role in controlling their populations (Baráz 2002).

## Data collection

Cameras were placed by Bükk National Park (NP) staff from May 2015 until August 2018. Location of the cameras were opportunistic and not fully random, as they were placed next to routes where there were previous observations of large mammals, especially wolf. Buffer zones ( $d=10$  km) were placed on each camera points in order to conceal the exact location of the camera due to high risk of theft (**Fig. 2.**).



**Figure 2.** Location of the Bükk National Park Directorate (study area: brown), Bükk National Park (protected areas: green) and camera traps locations (orange buffer zones ( $d=10$  km)) in Hungary.

NP broadened its camera stock each year, which resulted in observations from 8 cameras in 2016, 11 cameras in 2017 and 18 cameras in 2018. If the camera couldn't record valuable data for NP purposes (mostly presence-absence data) for consecutive months, it was then replaced by NP staff. The 3 years resulted in observations from 22 different sites.

From several recorded information by the camera, only time and date were registered for the study. Camera traps were set to point to routes that are frequently used by large mammals and several times to ephemeral ponds or wallows where ungulates often pay visits. For each location GPS coordinates were recorded.

Cameras used by the NP were all Reconyx: UltraFire XR6; HyperFire HC500, PC900 and PC800; RapidFire PM75.

### **Data analysis**

All photos and videos were analysed by using Windows' built in Photo Viewer: each time a focus species (wolf, fox, red deer, roe deer, wild boar) appeared on a footage, the site, the date and the timecode of the first footage was registered next to the name of the species and the number of individuals that could be counted during the stay of the animal(s). If it was possible, the age cohort (young or adult) and the sex (male or female) were registered too for further investigations (see Appendices - III. e.g. data sheet). All data was collected in Microsoft Excel.

In order to avoid overestimation of a species presence due to a prolonged stay of a single individual, every record of a same species within a 30-minute interval was considered as one individual, i.e. one independent event (Wearn et al. 2017). When it was possible to differentiate between individuals (e.g. different antlers, male - female), then these events became independent registrations, even if they did not exceed the 30-minute time limit. When individuals could not be differentiated from each other I used the 30-minute time frame.

Factors like timecode of the first footage and the name of the species from 2016, 2017 and 2018 were needed for the final calculations of activity overlaps. As the package defines the unit of time as a day (0-24 h) I needed to convert each time code to fit between 0 and 1 following the calculation below (Meredith and Ridout 2016).



1 day = 86400 sec.

TM = hour\*3600 + minute\*60 + sec

TM / 86400 = X

X then varies between 0 and 1.

In my analysis CET was used instead of solar time to be beneficial and convenient for local practitioners.

Final data analysis was carried out in R (Version 1.2.5033) by using the package “*overlap*”. This tool was designed to estimate the coefficient of overlapping by fitting kernel density functions to times of observations of animals. The coefficient of overlap is a quantitative measure ranging from 0 (no overlap) to 1 (identical activity patterns) (Ridout and Linkie 2009). When comparing the kernel density curves of two different species, the area lying under both density curves is  $\Delta$  (“*delta*”), the overlap coefficient.

The “spikiness” of the curves has an effect on the final delta value, thus we need to adjust it to the sample sizes. The “*overlap*” package operates with default built-in estimators to define the adjustment of the curves, but the user needs to choose the right one when writing the code. The best estimator depends on the size of the smaller of the two samples: when the smaller sample is less than 50, “*Dhat1*” performs better, while “*Dhat4*” is define for sample sizes greater than 75. I chose *Dhat1* for values bigger than 50 yet still smaller than 75. See **Table 1** and **2**.

For the estimation of confidence intervals, a special way of bootstrapping (i.e. the process when taking the existing sample as representation of the population and generating a large number of new samples by randomly resampling the original observations (Efron and Tibshirani 1985)) was used, called *smoothed bootstrap*. This operates by fitting a kernel density to the original data then draw random simulated observations from the distribution, so most simulated observations would fall in the same range, but a few will fall outside, creating a more “naturally distributed” simulated data (Faraway and Jhun 1990). The mean value of the smoothed bootstrap will be slightly different from  $\Delta$ , which is the *bootstrap bias*, that was taken into consideration when confidence intervals were calculated.

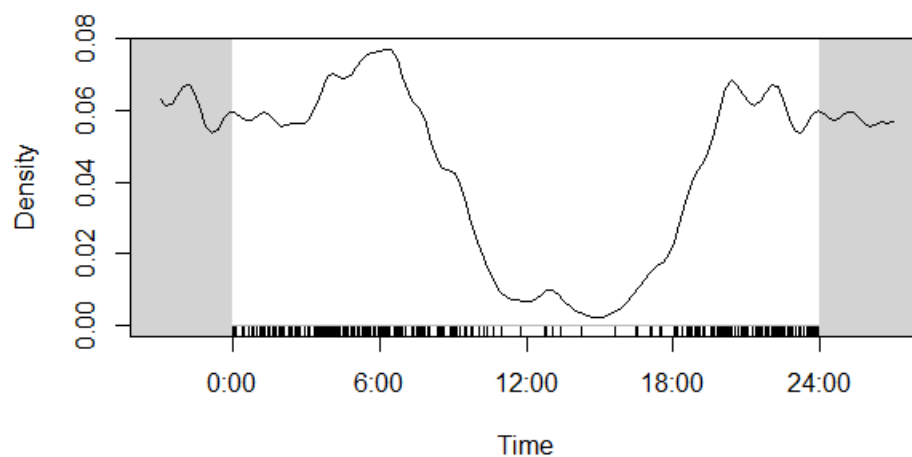
For life cycle comparisons, sensitive periods (rut, calving, summer and winter or wolves' pup-upbringing) were defined for wolf and its most consumed prey: roe deer, red deer and wild boar (Heltay 2000; Lanszki et al. 2012).

# Results

## Cumulative activity overlaps

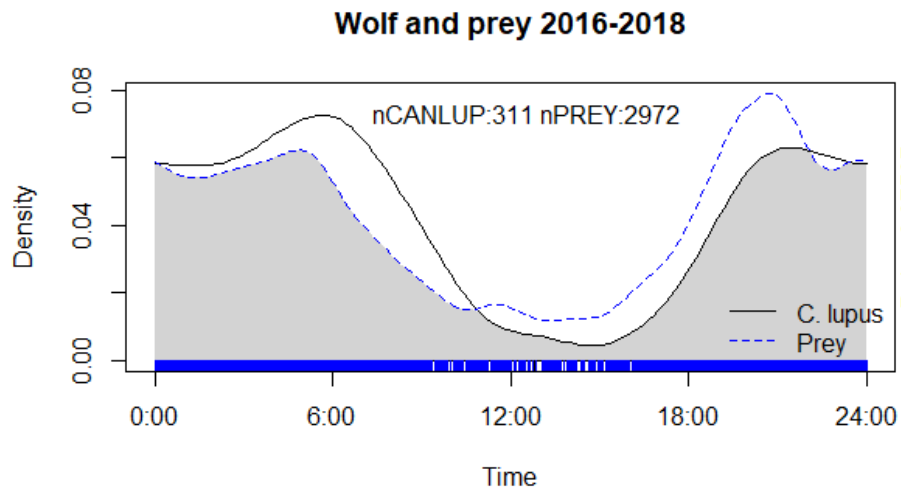
Across 32 months of camera trapping I was able to get 311 independent events of wolf and 2972 of its main prey: roe deer (n=808), red deer (n=1234), and wild boar (n=930).

80% of the total independent registrations of wolves fell between 18 p.m. and 6 a.m. Their daily cycle showed 2 activity peaks, one between 3 a.m. and 7 a.m. (35.7 % of total) and the other between 20 p.m. and 23 p.m. (25.1 % of total) and showed the lowest activity between 11 a.m. and 16 p.m. (3.2 % of total) (**Fig. 3**).



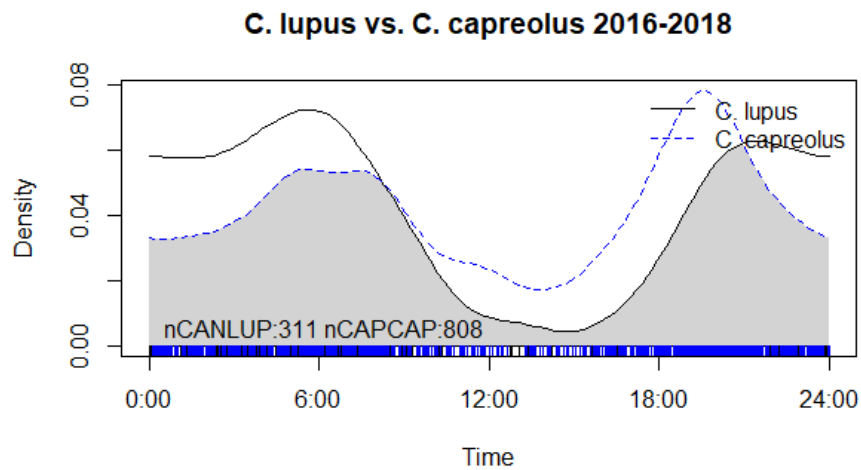
**Figure 3.** Daily activity period of wolf in Bükk National Park, Hungary (2016-2018).

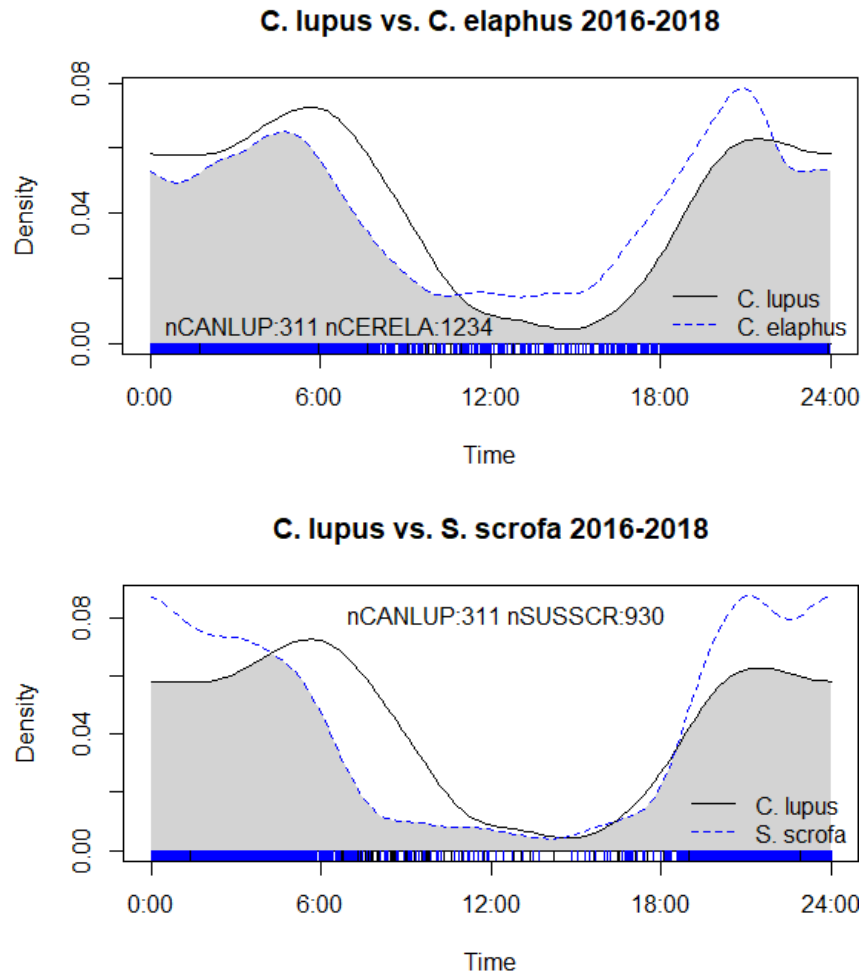
When functional groups were investigated, wolves' and preys' overlap were generally high ( $\Delta=0.77$ ; 95% CI [0.68-0.88]) (**Fig. 4**).



**Figure 4.** Activity pattern comparison between functional groups (blue dashed line=prey, black solid line=*C. lupus*) in Bükk National Park, Hungary (2016-2018).

Wolf activity range coincide the most with red deer ( $\Delta=0.87$ ; 95% CI [0.82-0.91]) and the less with roe deer ( $\Delta=0.79$ ; 95% CI [0.74-0.84]) in general (**Fig. 5**).





**Figure 5.** Differences between each prey species' (roe deer, red deer and wild boar) and the wolf's activity patterns (blue dashed line=prey species, black solid line=*C. lupus*) in Bükk National Park, Hungary (2016-2018).

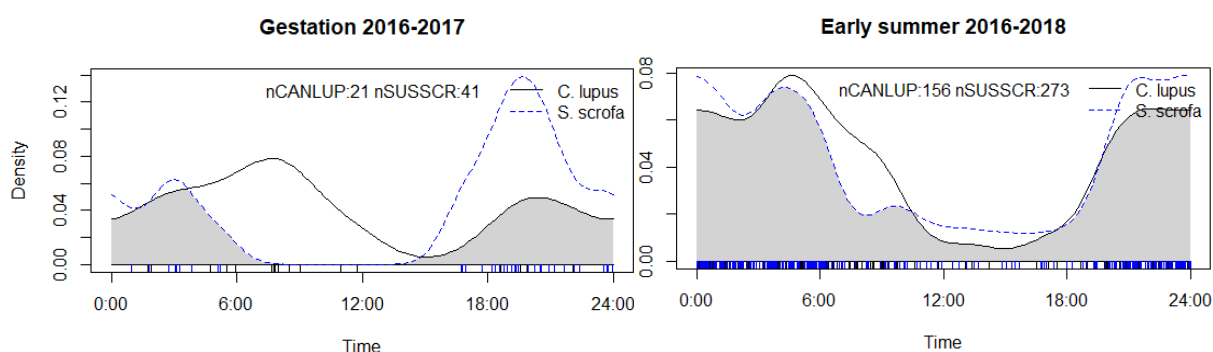
## Life cycle comparisons

Sixteen sensitive periods were defined for wolf and its most consumed prey, to be able to detect changes on a smaller scale (**Table 1**).

**Table 1.** Activity overlap coefficients ( $\Delta$ , **bold** highlights the lowest numbers) in different sensitive periods according to the species' life cycles in Bükk National Park, Hungary (2016-2018).

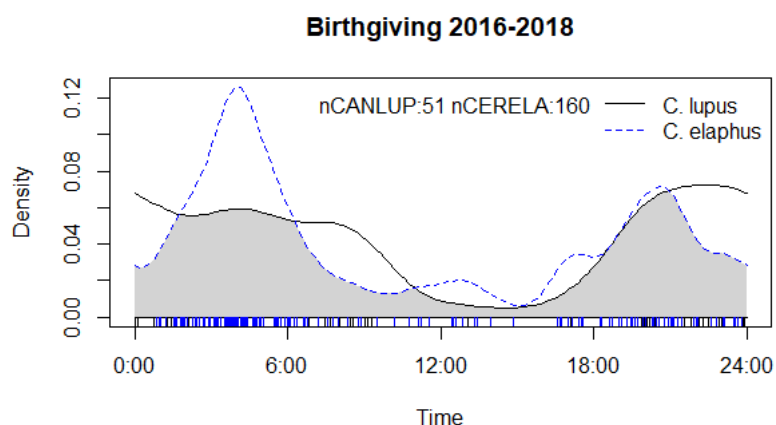
Species / Season	Period (months)	Estimator	n (prey)	<i>C. lupus</i>		
				n (wolf)	Estimate ( $\Delta$ )	95% CI
<i>C. capreolus</i>						
Winter	Nov - Febr	<i>Dhat1</i>	124	63	0.72	0.60-0.81
Wolf pup upbringing	Apr - Jun	<i>Dhat4</i>	312	139	0.81	0.73-0.87
Birthgiving	May - Jun	<i>Dhat4</i>	207	120	0.79	0.69-0.85
Rut	Jul – Aug	<i>Dhat1</i>	148	51	<b>0.64</b>	0.50-0.73
<i>C. elaphus</i>						
Winter	Nov - Febr	<i>Dhat1</i>	196	63	0.81	0.72-0.92
Wolf pup upbringing	Apr - Jun	<i>Dhat4</i>	407	139	0.8	0.70-0.85
Birthgiving	May	<i>Dhat1</i>	160	51	0.76	0.64-0.85
Pre-rut	Jul - Aug	<i>Dhat1</i>	307	51	0.8	0.73-0.92
Rut	Sep - Oct	<i>Dhat1</i>	278	52	0.79	0.70-0.92
<i>S. scrofa</i>						
Gestation	Jan - Febr	<i>Dhat1</i>	41	21	<b>0.5</b>	0.35-0.73
Birthgiving	Febr - Apr	<i>Dhat1</i>	128	45	<b>0.66</b>	0.52-0.79
Winter	Nov- Febr	<i>Dhat1</i>	178	63	<b>0.65</b>	0.53-0.76
Wolf pup upbringing	Apr - Jun	<i>Dhat4</i>	178	139	0.81	0.74-0.90
Early summer	May - July	<i>Dhat4</i>	273	156	0.87	0.82-0.95
Solitary males	Aug - Oct	<i>Dhat1</i>	382	55	0.86	0.80-0.97
Breeding	Nov - Dec	<i>Dhat1</i>	137	42	<b>0.65</b>	0.49-0.77

On smaller scales, wild boar activity showed the least overlap with wolf among all the ungulates in study. This temporal segregation was the most expressed at around its reproductive period, especially at gestation ( $\Delta=0.5$ ; 95% CI [0.35-0.73]). Early summer and autumn, when males are separated from the group, did not differ significantly to each other and from the other two ungulates in study ( $\Delta=0.87$ ; 95% CI [0.82-0.95] and  $\Delta=0.86$ ; 95% CI [0.80-0.97], respectively) (**Fig. 6**).



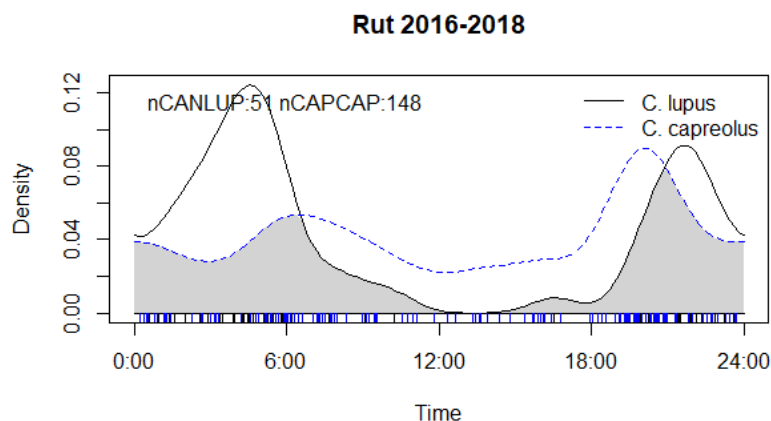
**Figure 6.** Lowest and highest activity range overlap between wild boar and wolf (blue dashed line=*S. scrofa*, black solid line=*C. lupus*) in Bükk National Park, Hungary (2016-2018).

Red deer activity was followed by wolf activity throughout the years, however in May, when calves are born, a peak appeared around 4 a.m. in their daily rhythm. This period showed the lowest overlap, too ( $\Delta=0.76$ ; 95% CI [0.64-0.85]) (**Fig. 7**).



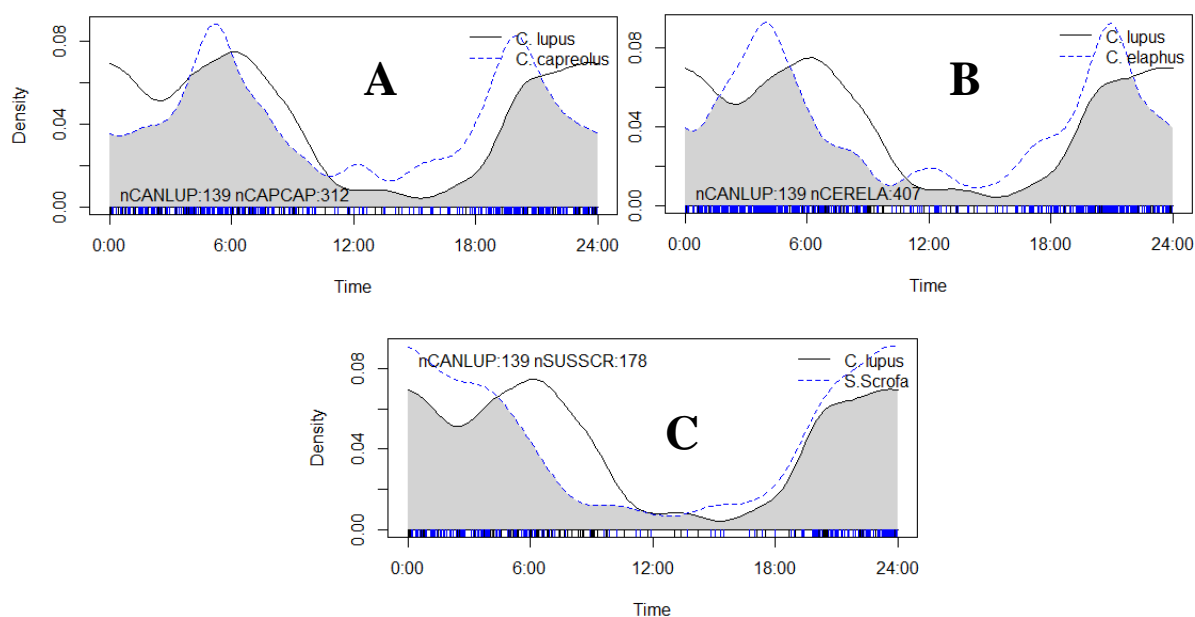
**Figure 7.** Activity range overlap between wolf and red deer (blue dashed line=*C. elaphus*, black solid line=*C. lupus*) in May in Bükk National Park, Hungary (2016-2018).

Roe deer, in general, showed smaller overlap with wolf than red deer ( $\Delta=0.87$ ; 95% CI [0.82-0.91] and  $\Delta=0.79$ ; 95% CI [0.74-0.84], respectively). At the time of rut, roe deer showed the second lowest overlap ( $\Delta=0.64$ ; 95% CI [0.50-0.63]) in the study (**Fig. 8**).



**Figure 8.** Activity range overlap between wolf and roe deer (blue dashed line=*C. capreolus*, black solid line=*C. lupus*) in rutting season (July-August) in Bükk National Park, Hungary (2016-2018).

Ungulates activity period overlaps with their predator at the time of wolf pup-upbringing, moreover it is generally high and are almost equal (roe deer:  $\Delta=0.81$ ; 95% CI [0.73-0.87]; red deer:  $\Delta=0.8$ ; 95% CI [0.70-0.85] and wild boar:  $\Delta=0.81$ ; 95% CI [0.74-0.90]) (**Fig. 9**).

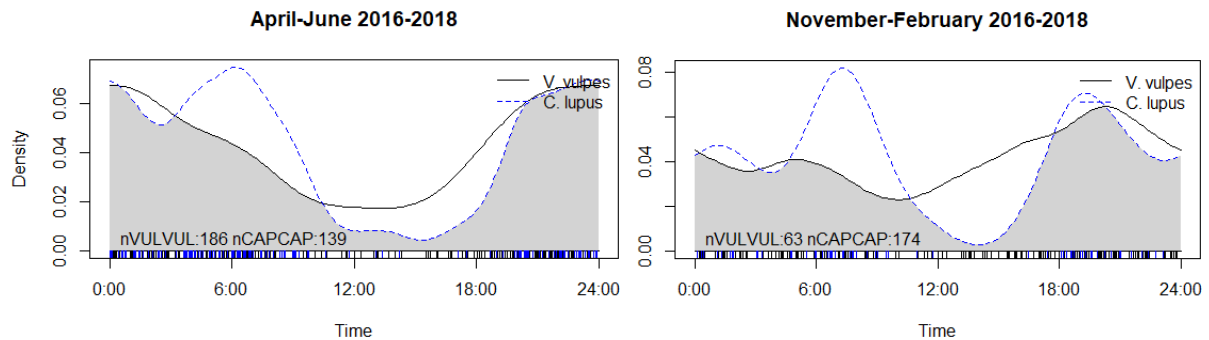


**Figure 9.** Activity range overlaps (blue dashed line=prey species, black solid line=*C. lupus*) between wolf and roe deer (A), red deer (B) and wild boar (C) at the time of wolves' pup-upbringing (April-June) in Bükk National Park, Hungary (2016-2018).



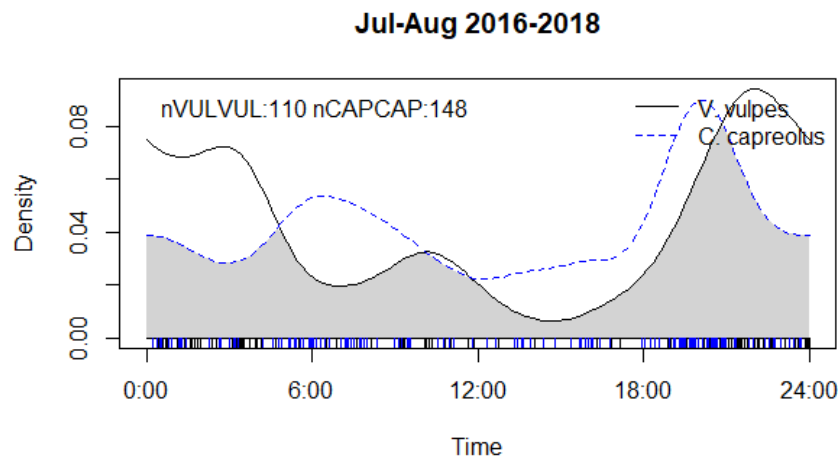
## Intraguild competition

Activity overlap between wolf and red fox is generally high all year, however the highest is at spring-early summer ( $\Delta=0.83$ ; 95% CI [0.77-0.93]) and the lowest is at winter ( $\Delta=0.77$ ; 95% CI [0.68-0.88]) (**Fig. 10, Table 2**).



**Figure 10.** Activity range overlaps between wolf and fox (blue dashed line=*C. lupus*, black solid line=*V. vulpes*) at spring and wintertime in Bükk National Park, Hungary (2016-2018).

Fox showed generally high overlap with roe deer, the lowest at the time of rutting, which is also the first months of the newborn fawns ( $\Delta=0.74$ ; 95% CI [0.61-0.80]) (**Fig. 11**).



**Figure 11.** Activity overlap between fox and roe deer (blue dashed line=*C. capreolus*, black solid line=*V. vulpes*) at its rutting period in Bükk National Park, Hungary (2016-2018).

Results of activity overlap analysis between the two carnivorous species (wolf and fox) and fox and the only large herbivore it might consume (roe deer) are shown in **Table 2**.

**Table 2.** Activity overlap coefficients ( $\Delta$ ) in different sensitive periods according to the species' life cycles, throughout 3 consecutive years (2016-2018). Bold numbers represent the lowest values.

Species / Season	Period (months)	Estimator	n	<i>V. vulpes</i>		
				n (fox)	Estimate ( $\Delta$ )	95% CI
<i>C. lupus</i>						
Wolf pup rearing	Apr - Jun	<i>Dhat4</i>	186	139	0.83	0.77-0.93
Summer	Jul - Oct	<i>Dhat4</i>	160	91	0.80	0.71-0.91
Winter	Nov - Febr	<i>Dhat1</i>	63	174	<b>0.77</b>	0.68-0.88
<i>C. capriolus</i>						
Winter	Nov - Febr	<i>Dhat4</i>	124	174	0.80	0.70-0.87
Spring	Mar - Apr	<i>Dhat4</i>	165	90	0.84	0.79-0.96
Birthgiving	May - Jun	<i>Dhat4</i>	207	133	0.77	0.66-0.82
Rut	Jul - Aug	<i>Dhat4</i>	148	110	<b>0.74</b>	0.61-0.80
Post -rut	Sept - Oct	<i>Dhat1</i>	164	50	0.76	0.67-0.89

# Discussion

Activity pattern analysis revealed that wolf and its prey species appear at similar time periods on the camera trap footages, so the degree of overlap between the functional groups (prey-predator) is high ( $\Delta=0.77$ ) (**Fig. 4**). Inherently, wolves need to meet ungulates to prey on them, thus some level of overlap is inevitable.

When individual species were surveyed, I still did not find highly variable differences between their overlap with wolves'. All three ungulate species (roe deer, red deer, wild boar) showed a relatively high overlap in their activity with the wolf. Wolf's activity range coincide the most with red deer's ( $\Delta=0.87$ ) and the less with roe deer's ( $\Delta=0.79$ ) during the 3 years of the study (2016-2018). This suggests a relatively high activity overlap of wolf and its 3 commonly occurring ungulate prey species in Bükk National Park, Hungary.

This does not mean, however, that activities of these species should overlap the same way during the whole year. Based on my study, it is possible to observe some sensitive periods in roe deer's and wild boar's life cycle which result in temporary lower overlap coefficients. Temporal segregation appeared only on these smaller timescales, which suggests that at special periods of the year some species indeed try to avoid their predators as much as possible (or predators are less likely to focus on these species in these periods, see below).

Wild boars showed the least overlap ( $\Delta=0.5$ ) at the time of gestation and when piglets are born (**Fig. 6**). This could be either interpreted as boars try to be cautious and avoid wolves or that they are so aggressive and protective for their young these times that wolves rather choose other prey as the risk of getting injured is possibly high. Wild boar in some countries is not the favoured prey species for the wolf, probably due to its high risk to get injured when prey upon without the support of the pack (Patkó, pers. comm.). Interestingly, based on literature, it seems that wild boar is readily available among the food items of the wolf during the spring period, however Wagner et al. (2012) attributes this seasonal difference to the positive selection of juveniles compared to the risky, well-fortified adult wild boars. In my study, activity overlap with wild boar was one of the lowest when the piglets born, however it was followed by the highest values ( $\Delta=0.87$ ) when piglets were few months old – this might

mean, that wolf does prey upon piglets, but only when the risk of getting injured by the aggressive females is lower. This, however, should be further investigated by feeding habit studies in this period.

Second lowest overlap was between wolf and roe deer at rutting period ( $\Delta=0.64$ ) (**Fig. 8**) while interestingly, at its rutting period, red deer showed high overlap with wolves ( $\Delta=0.79$ ) (**Fig. 7**). Laundré et al. (2001) found no increase in vigilance level in the Yellowstone National Park after the re-introduction of wolf in male elk (*Cervus elaphus*) and bison (*Bison bison*) compared to female elks. They explained it as male elks and bison face less predation than females simply by their larger size, which was also supported by data on the sex composition of elk killed by wolves in the park. On the other hand, males have a higher reproduction pressure, as they would lose more from reduction in feeding (i.e. increased vigilance) than gain from increased surveillance. Red deer can afford rut in co-existence with wolves, while such a conspicuous act in the case of the smaller bodied roe deer would cause a presumably risky encounter with its predator. This could be the reason for the high difference in activity overlaps at their rutting periods for roe deer and red deer. Similar observations were confirmed by Wagner et al. (2012) in Germany, where wolves preferred hunting on juvenile to adult red deer while roe deer consumption showed no age-based selection. Thus, roe deer needs to find a way to minimize the chance of encounters with wolves at the time of rut and this could be done by temporal segregation next to increased vigilance and typical barking behaviour (Reby et al. 1999).

On the other hand, July and August are the first months of the newborn fawns (born in May-June (Heltay 2000)) which would be easy targets for adult wolves to prey upon – being not in synchrony with the possibly easiest food source also suggests, that at this period roe deer actively avoid encounters with wolves, rather than wolf disavouring roe deer. These low values, however, are still above  $\Delta=0.5$  and we have to be careful when interpreting the results (e.g. this does not mean that wolves and roe deer cannot coexist spatially and temporally, cf. hunters opinion below).

During interpretation, firstly we need to consider that, many other things besides predator presence can influence the normal activity of a species. There are several studies that reported human-driven landscape and community impacts – such as change in land-use (Ramesh and

Downs 2013), human activity (Ngoprasert et al. 2017; Nix et al. 2017; Wang et al. 2015), hunting (Bitetti 2008), predator control (Brook et al. 2012) or the presence of an invasive competitor or predator (Gerber et al. 2012) – may change species' activity patterns through altered temporal niche partitioning.

Also, little is known about the actual food preference of the wolf. There was a study about the diet of Hungarian wolves from a different national park that based mainly on microscopic analysis of wolf scats ( $n=81$ ) (Lanszki et al. 2012). Main disadvantage of these kinds of studies is that the results are not undoubtedly the direct consequences of actual hunts of the pack, as faeces can contain remains of opportunistically consumed carcasses. What we see in the manifestation of temporal segregation in the activity periods could simply be the disfavour of the species as food resource at certain times of the year by the wolf and not necessarily the result of the preys' active avoidance.

Generally high overlap, even at the time when adult wolves have to hunt the most (i.e. at pup-upbringing when pups are already eating solid food while at the same time are still not able to hunt on their own), also suggests that wolves are the ones that more successful in synchronizing their activity with the prey, rather than temporal segregation would be a general solution for prey to avoid encounters.

However, at sensible periods of the year, ungulates might strengthen their chances to elude wolves by getting active at times when predators generally not active, like in the case of red deer having an activity peak at 4 a.m. during the calving period (**Fig. 7**).

Regarding intraguild competition and according to Bassi et al. (2012), there is only a low and seasonal overlap in the diet of wolves and foxes and that mostly exhibited when newborn roe deer fawns are available. There is a constant high activity overlap (lowest:  $\Delta=0.77$ ; highest:  $\Delta=0.83$ ) between the species regardless the seasons and prey availability which implies that the two species can co-exist and the competition between them is rather neglectable. This also suggests that the presence of fox, even though they are able to predate fawns (Bassi et al. 2002), is not a considerable source of fear for roe deer (**Table 2**).

To conclude, camera trap footages suggest that predator and prey species can co-exist in Bükk Mountains, Hungary. Thus hunters concern on how wolf's presence disturb ungulate species (Højberg et al. 2017; Patkó, pers comm.) is not completely confirmed as the lack of temporal segregation likely contribute to possible encounters. However, in critical periods of the year, such as rutting or birthgiving, these observations might be temporarily true. To fully understand this complex and dynamic behaviour system, further investigations with different spatially and temporally synchronyzed study designs (e.g. vigilance level (Laundré et al. 2001), landscape of fear (Brown et al. 1999) and feeding habit (Lanszki et al. 2012)) are needed.

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# Chapter 3 - Prey-predator density estimations in Bükk National Park, Hungary

## Abstract

Non-invasive camera traps are handful tools for wildlife management as they are relatively cheap, durable and make constant, long-term monitoring possible while not disturbing the normal behaviour of the target species. As they are becoming more ubiquitous for wildlife managers, new, statistics-based approaches emerge to broaden the spectrum of utilization of these cameras. One of them is the Random Encounter Model (REM) that makes population density estimation possible without the need of individual recognition.

Large carnivores have the potential to influence the density of their prey species, especially in new areas what they are just about to re-colonize. Globally, wildlife management use several techniques parallel to accurately monitor these fluctuations in population densities. I have tested if in Hungary REM could be a part of the currently used toolkit for nature conservationists and game wardens. My results indicated similar results than the reference densities from the area ( $STRn=14$  while  $REM\bar{n}=16$  individuals;  $\overline{SD}= 1.28$  individuals) thus REM has the potential to become a nation-widely acknowledged analytical tool – however the study layout needs fine-tuning and several small details should be incorporated into the field design if in the future a national park or a hunting association want to lean exclusively on camera based REM monitoring.

# Introduction

Re-appearing large carnivores is a relatively new event in many European countries (Chapron et al. 2014). The situation is the same in Hungary, where wolf (*Canis lupus*) and lynx (*Lynx lynx*) populations are stable and slowly increasing in the last 50 years and re-colonize new areas where both resident fauna and people “forgot” the rules of co-existence (Szemethy et al. 2004). One impact that these carnivores could put on their naïve prey is to lower their numbers by direct predation.

Thus, estimating population size and density for large carnivores and their prey is particularly important for their monitoring, conservation and management. There are several options for wildlife managers and national parks (NP) to do so, which measures could be categorized as invasive or non-invasive methods (Long et al. 2008). Because large carnivores are usually protected species and present only at low densities within a large territory, also because they are nocturnal, elusive and not to mention that they are potentially aggressive, they are not ideal subjects for invasive methods (Long et al. 2008; Patkó et al. 2016). Non-invasive methods, however, that usually do not require the physical contact with the animal and do not disturb their normal activities and behaviour, can prove to be useful measures for monitoring these animals. Camera traps, for instance, are popular choices for wildlife managers for constant, long-term monitoring due to its relative cheap price. For a long period camera-traps were mostly used for presence-absence or behavioural studies but in the last 2 decades more and more statistical approach was developed to include these data into everyday game management practice (Rowcliffe et al. 2008; Nakashima et al. 2018).

One of these is the Random Encounter Model (REM) that gives population density estimations solely based on camera trap data, without the need of individual recognition of the animals. The model operates with three assumptions: (i) the movement of the individual is random; (ii) captures correspond to independent contacts between cameras and the animals; and (iii) the population is closed (Rowcliffe et al. 2008). The most problematic constraint of the model is that it is based on the theory that animals move like ideal gas particles, roaming randomly and independently of each other. Animals, however, constantly monitor their habitat, align their behaviour with the physical environment and react to each other. Yet, the

model was found robust against most of the violations of the basic assumptions, although the “human factor”, i.e. the choice of some of the variables in the model, like daily travel speed, or in some cases the group size, still plays a significant role in the final results (Rowcliffe et al. 2008). The model has been tested on various species, such as native and invasive hares in Ireland (Caravaggi et al. 2016), on small and elusive carnivores, like pine martens in Italy (Balestrieri et al. 2016) or large and potentially dangerous carnivores, like lions in Tanzania (Cusack et al. 2015) or brown bears in Bulgaria (Popova et al. 2018), yet in Eastern-Europe these methods are still not wide-spread and ubiquitous in wildlife management.

No matter how important sound science should be in managing such controversial animals, like large carnivores, Hungary has not yet accepted a nation-widely used standardized protocol in its large carnivore monitoring system. National parks usually use DNA information from scats to define the number of the current wolf population (Hausknecht et al. 2010; Stéger 2019) but unlike camera-traps, this method requires more human resources and time to collect enough samples, it is more expensive (Long et al. 2008) and does not make it possible to compare shorter periods to each other (e.g. summer vs. wintertime or reproduction season vs. upbringing season). Not to mention that collecting scats, that are usually the markers of territory edges, from trails can lead to extra energy investment by individuals to protect their territory against intruders (Brzeziński and Romanowski 2006).

In this study I am going to make the first attempt in Hungary to assess a NP collected dataset through the Random Encounter Model in order to develop a new measure for Hungarian wildlife management and conservation for getting a cheap, reliable and fast way to estimate large mammal population densities.

# Materials and methods

## Study area

The study area was (**Fig. 2**) within the Bükk National Park that is located on the north-eastern part of Hungary with the area of 42 296 ha (390.63 km<sup>2</sup>). The area is considered as a high elevation habitat, despite of the highest points of the Bükk Mountains are still below 1000 m (highest peak is Istállóskő with 959 m), yet there are 50 which are still above 900 m.

The area is covered with a deciduous forest (94%) with the constitution of European beech (*Fagus sylvatica*) (35%), Sessile oak (*Quercus petraea*) (32%), European hornbeam (*Carpinus betulus*) (13%) and Turkey oak (*Quercus cerris*) (7%) (Baráz 2002) (**Fig. 1**).

The weather has a significant continental influence, which results in warm summers and cold winters (average January temperature is -4 °C) and the most snowy days in the country. Despite of two precipitation maximum and the total annual precipitation of 773 mm, the Bükk Mountains are nonetheless poor in rivers or still water bodies. The average annual temperature is approximately 2 °C lower than the national average, which equals to 7-8 °C degree here.

The Bükk National Park and the surrounding areas are rich in vertebrates and many of them are protected in Hungary with several Carpathian species. High numbers of large herbivores create a lot of conflicts between conservationists and forestry – returning large carnivores, like the wolf or the lynx , could play an important role in controlling their populations (Baráz 2002).

## **Data collection**

Camera trap data was retrieved on the 23<sup>rd</sup> of August, 2018, from Bükk National Park Directorate (NP) zoology department. Cameras were placed by NP staff from May 2015 until August 2018. Cameras were placed next to routes that were proved to be used by large mammals, especially wolf. Once a camera did not provide useful information on wolves then it was removed to other location. Buffer zones (d=10 km) were created on the exact camera locations in the GIS map, in order to avoid theft or damage of the devices. (**Fig. 2**). Buffer zone is arbitrary and not used during any of my analysis.

Camera stock increased each year, which resulted in 6 (2016), 10 (2017) and 11 cameras (2018), respectively. The 3 years resulted in observations from 22 different sites, including routes that are frequently used by large mammals, or ephemeral ponds or wallows where ungulates often pay visits.

Cameras record plenty of useful information about the environment (moon cycle, temperature, etc.), yet only time, date and GPS coordinates were registered for this study besides the species and the amount of animals on the footage.

Cameras used in the study were all Reconyx: UltraFire XR6; HyperFire HC500, PC900 and PC800; RapidFire PM75.

## **Data analysis**

All photos and videos were then analysed in Windows' built in Photo Viewer. I registered the species, the site, the date and the timecode of the first footage every time a focal mammal appeared on a record. I also counted the amount of the individuals that appeared on the footages, also, if it was possible, the age cohort (young or adult) and the sex (male or female) were registered too for further investigations.

To be able to estimate density based on Radom Encounter Model (REM) from camera trap data, biological variables and camera characteristics are needed. The REM is a method based on Rowcliffe et al. (2008), for estimating animal density from camera trap data without the need for individual recognition.

$$D = \frac{y}{t} \cdot \frac{\pi}{Vr(2 + \theta)}$$

where:

D = population density (individuals/km<sup>2</sup>);

y = total number of independent registrations;

t = survey effort (i.e. total camera days);

r = radius of the detection zone of the camera trap (km);

θ = angle of the detection zone of the camera trap (radians);

v = mobility of the species (km/day).

Mobility for focus species are based on literature, as it was not possible to obtain Hungarian telemetry data for the focal species. Therefore, I used data from the international literature, focusing on studies of the same species under similar conditions, following Rowcliffe et al. (2008). Travel speeds were defined as the following: Grey wolf - 24.85 km/day (Jedrzejewski et al. 2001); roe deer - 0.992 km/day (Chapman et al. 1993); red deer - 1.984 km/day (Pépin et al. 2009); wild boar - 5.763 km/day (Janeau et al. 2014). Camera characteristics were constant throughout the analysis:  $\theta=0.698$  rad;  $r=0.03$  km (retrieved from RECONYX manual).

Camera characteristics ( $r$  and  $\theta$ ) were retrieved from camera trap manuals, following Popova et al. 2018. Data was analysed in R (Version 1.2.5033) by using the R package “*remBoot*”.

The absolute minimum number of independent registrations according to Rowcliffe et al. (2008) is 10, whereas 20 and above are recommended. Likewise, minimum 500 camera days are needed to get accurate results. For this purpose, I defined a similar period in each year when I expected for the most wolves to appear on the footages. Wolves leave pups at so-called “*rendez-vous sites*” after the abandonment of dens when the pack is out for hunting (Murie 1944). According to Capitani et al. (2006), in the north-eastern Apennines this period is somewhere between the 15<sup>th</sup> of June and the 30<sup>th</sup> of September, and this is approximately

the situation in Hungary (Patkó pers. comm.). Following these observations, I analysed footages between the 1<sup>st</sup> of June till the 30<sup>th</sup> of September.

The REM is not time-sensitive regarding to the repeated registrations of the same individual, thus individual recognition is not an issue that should be taken into consideration when it comes to data analysis (Rowcliffe et al. 2008). For the calculation of standard deviation and confidence intervals bootstrapping (Efron and Tibshirani 1985) was used.

All GPS coordinates were registered in QGIS (ver. 3.10 “*A Coruña*”), and a polygon with a 24.85 km buffer (i.e. the biggest value for daily travel speed amongst the species in study) was created to calculate the area covered by the cameras.



# Results

## Basic data collection for REM

I used the records of 6 cameras from 2016, 10 cameras from 2017 and 11 from 2018. This resulted in 587 camera days in 2016, 792 in 2017 and 660 in 2018. This amount of time was enough to get 30 independent registrations of wolf in 2016, 43 in 2017 and 94 in 2018. Four cameras (out of six, 66%), 8 cameras (out of ten, 80%) and 6 cameras (out of eleven, 54.5%) recorded wolf in 2016, 2017 and 2018, respectively. Pups were recorded in all 3 years which is a direct proof that wolf breeds in the Bükk National Park.

Throughout the 3 years of the study, out of 4292 positive record (i.e. when camera was triggered by an animal and not by a vehicle, humans, or weather) 3993 (93%) could be identified. This was made up by 15 species. The most frequently seen species on the footages was red deer (1234 events, 30.9%), followed by wild boar (930 events, 23.3%), and roe deer (808 events, 20.2%). Grey wolf registrations were relatively low compared to all registrations (311 events, 7.8%), similar to red fox (557 events, 13.9%) which appeared slightly more often in front of the cameras. Less observation were about European hare (*Lepus europaeus*), marten (*Martes spp.*) and lynx (*Lynx lynx*) (27, 2 and 1 footages, respectively).

All cameras, together with their buffer zone ( $d=24.85$  km) covered  $197\text{ km}^2$  which is equal to approximately 45.7% of the total area of the national park. It is worth noting that this area is not completely covered by forests, as there are three villages within the protected zone, thus our study area only roughly covered the half of the NP.

### Population density estimations (REM)

Wolf mean density for the 3 years (2016-2018) is 0.128 individual/km<sup>2</sup> ( $\overline{SD}$ =0.010) that suggests there were  $\bar{n}$ =25 individuals ( $\overline{SD}$ =27-23 ind.) within the National Park (390.63 km<sup>2</sup>). According to ungulates, the highest mean density belongs to red deer ( $\overline{REM}$ =8.920;  $\overline{SD}$ =0.474) that implies  $\bar{n}$  = 1757 individuals within the borders of the NP. Lowest density belongs to wild boar ( $\overline{REM}$ =4.621;  $\overline{SD}$ =0.359), which would be equivalent to  $\bar{n}$  = 910 individuals each year in the study area. The model predicted  $\bar{n}$  = 1382 individuals in the NP ( $\overline{REM}$ =7.013;  $\overline{SD}$ =0.221) in the case of roe deer. The Random Encounter Model density estimations for wolves and its main prey species are indicated in **Table 3**.

**Table 3.** Estimations of the Random Encounter Model (REM) for population densities of wolf and its main prey species: red deer, roe deer and wild boar in Bükk National Park, Hungary (2016-2018).

	Species	Independent registrations	REM estimation (individual/km <sup>2</sup> )	CI upper (95%)	CI lower (95%)	SD
<b>2016</b>	<i>C. lupus</i>	30	0.079	0.079	0.079	0.009
	<i>C. capreolus</i>	118	7.812	7.821	7.811	0.252
	<i>C. elaphus</i>	332	10.999	10.998	10.975	0.596
	<i>S. scrofa</i>	415	4.729	4.733	4.719	0.339
<b>2017</b>	<i>C. lupus</i>	43	0.085	0.085	0.085	0.004
	<i>C. capreolus</i>	216	10.657	10.661	10.648	0.353
	<i>C. elaphus</i>	471	11.644	11.650	11.631	0.492
	<i>S. scrofa</i>	693	5.886	5.897	5.878	0.480
<b>2018</b>	<i>C. lupus</i>	94	0.220	0.220	0.219	0.018
	<i>C. capreolus</i>	44	2.569	2.572	2.569	0.057
	<i>C. elaphus</i>	141	4.117	4.123	4.110	0.335
	<i>S. scrofa</i>	323	3.247	3.253	3.243	0.259

Wolf densities increased drastically by 2018, while roe deer and red deer densities seemed to fall compared to the previous years.

For comparison with reference densities, values are shown in **Table 4**.

**Table 4.** REM estimations compared to reference densities for each focus species in Bükk National Park, Hungary (2016-2018).

	Species	REM estimation (individual/ km <sup>2</sup> )	SD	Individual/ area total (390.63 km <sup>2</sup> )	Reference densities	Source for reference
<b>2016</b>	<i>C. capreolus</i>	7.812	0.252	1538.9	765	Egererdő Zrt. (National Forestry - Game management data)
	<i>C. elaphus</i>	10.999	0.596	2166.8	690	Egererdő Zrt. (National Forestry - Game management data)
	<i>S. scrofa</i>	4.729	0.339	931.6	515	Egererdő Zrt. (National Forestry - Game management data)
	<i>C. lupus</i>	0.079	0.009	15.6	14	Stéger et al. (2019)
<b>2017</b>	<i>C. capreolus</i>	10.657	0.353	2099.4	680	Egererdő Zrt. (National Forestry - Game management data)
	<i>C. elaphus</i>	11.644	0.492	2293.9	615	Egererdő Zrt. (National Forestry - Game management data)
	<i>S. scrofa</i>	5.886	0.480	1169.5	470	Egererdő Zrt. (National Forestry - Game management data)
	<i>C. lupus</i>	0.085	0.004	16.7	14	Stéger et al. (2019)
<b>2018</b>	<i>C. capreolus</i>	2.569	0.057	506.1	700	Egererdő Zrt. (National Forestry - Game management data)
	<i>C. elaphus</i>	4.117	0.335	811.0	680	Egererdő Zrt. (National Forestry - Game management data)
	<i>S. scrofa</i>	3.247	0.259	639.7	667	Egererdő Zrt. (National Forestry - Game management data)
	<i>C. lupus</i>	0.220	0.018	43.3	14	Stéger et al. (2019)

## Discussion

In spite of the fact that the number of cameras used was slightly under the recommended ( $n=11$  in 2018, instead of 20 recommended by Rowcliffe et al. (2008)), I was able to produce enough individual observations for all species through 12 months of the study in order to run REM analysis.

According to ungulate species, the model's predictions were quite different from the reference densities, despite of Egererdő's slightly larger area (app.  $230 \text{ km}^2$ ) (Egererdő introduction 2020). Egererdő's ungulate estimations are made in February each year, mostly based on the harvest bag from the previous year while taking all other signs into account, such as tracks, droppings, natural mortality and observations of juvenile and adult individuals (Nagy, pers. comm.). These are regular techniques in game management units in Hungary (Patkó pers. comm.; Szemethy 2020), that can be considered rather as an index for population dynamics than an accurate data on their density.

The problem is not unprecedented, yet a very common issue in the former Soviet Union, where the approaches and principles, upon which game management is based, have remained unchanged for the past 50 years (Apollonio et al. 2017). In these countries the population size is estimated from censuses of direct and indirect methods which methods are proved to be not reliable and with low accuracy (Apollonio et al. 2017; Morellet et al. 2007). Also, most censuses are based on abundance indices, which are then directly transformed into population numbers, however, due to the unknown relationship between abundance indices and true population size or how the environment complex affects the population, this is a serious statistical bias that should be avoided (Anderson 2003; Witmer 2005). An important goal of European ungulate management is to increase the scientific database of wildlife management, opposed to rely entirely on opinion or experience-based management systems (Apollonio et al. 2017). The REM could ease the issue with constant, independent cross-check for the abundance indices and direct censuses.

According to the Random Encounter Model, the wolf population density in the study area is between 0.079-0.220 individual/km<sup>2</sup> which is equal to a scale of 16-43 individuals respectively, in the area covered by the cameras, as the cameras, together with their buffer zone, covered approximately 197 km<sup>2</sup>. So, we can say that during the 3 years of the study the number of wolves was 25 individuals ( $\overline{SD}$ =1.97 individuals) in Bükk National Park (**Table 5**).

There are a few reasons why my estimation can differ from BNPD's own estimations. The REM survey is a bit above (n=25) the results of the genetic analysis that could identify 14 different individuals – however sample size was rather low in that study (n=21) (Stéger 2019). In the beginning of 2020, a census was carried out (BNPD census, 2020) that could identify 9-11 individuals from snow tracks and visual observation, thus the size of the pack seems to reduce by the end of a given year. Natural mortality (adult: 20%; young of the year: 45%, pups: 57-94% (Boitani 2000)) and poaching (BNPD poaching, 2018) takes away several individuals each year from the pack, while the mean litter size varies between 1-11 pups (Boitani 2000) thus 20-25 individuals with potential newcomers and satellite individuals are a possible scenario at the times of my study (June-September).

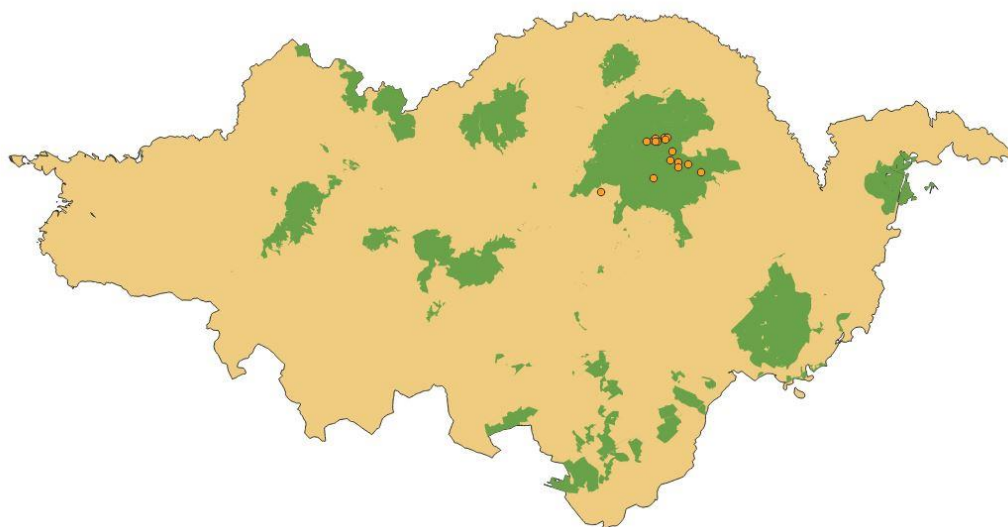
According to the National Park professionals, there is only one pack in my study area in Bükk mountains (Gombkötő, pers. comm.). Boitani et al. (2000) estimated the average pack size in Europe is 7 (2-15 individuals) but the final number strongly correlates with productivity, the success of dispersion, prey density and human influence, especially. According to this conclusion, there is a chance that the high numbers of independent registration of wolves in 2018 is because there were already two reproducing packs.

Another, even more possible scenario of the higher REM results, is that the study design was biased year by year by turning more into a non-random sampling as cameras were placed more accurately to routes that were previously proved to be frequently used by wolves (Gombkötő, pers. comm.). This could have been also contributed to the uneven number of registrations of ungulates during the study as NP mostly focused on carnivores when installed the cameras. Cusack et al. (2015) encountered a similar problem when they tried to estimate lion (*Panthera leo*) density in the Serengeti National Park, Tanzania, where due to habitat characteristics, cameras were often placed on trees which attracted lions seeking shadows during the day. When they compared their results to reference densities it was straightforward

that when daytime photos were included in the REM, that put a significant bias on the final estimation (e.g. 0.467 ind/km<sup>2</sup> compared to 0.142 ind/km<sup>2</sup> while reference density was 0.124 ind/km<sup>2</sup> for the same habitat-season analysis).

The original REM study by Rowcliffe et al. (2008) faced a similar issue when cameras, in order to avoid taking photographs of people strolling around on the open lawns of the study area, were placed on routes which were less visited by humans – and, for the same reason, also by one of the focal species of the study (Mara, *Dolichotis patagonum*) that preferred grazing on open lawns. This resulted in a clear underestimation of the species. A very important assumption of the model, namely that animals move independently of the cameras, is violated when the field design either avoid or target the focal species. There is very high chance that this contributed to the slightly overestimation of ungulate species in the first two years in my study, while wolf became overestimated by the 3<sup>rd</sup> year of the study. Being aware of this serious bias, using the data from the first two years might result in more reliable estimation (wolf:  $\bar{n}$ =16 individuals;  $\overline{SD}$ = 1.28 individuals; reference density: 14 ind. (Stéger 2019)) than including 2018 in the analysis in case of the wolf.

The genetic study (Stéger 2019.), that served as a reference for my study, was carried out across the whole area of the National Park Directorate (NPD), which is way bigger than the National Park (NP) itself: the total area of the NPD is 8847 km<sup>2</sup> while the NP, that incorporates my study site, covers only 431 km<sup>2</sup> (**Fig. 12**).



**Figure 12.** Area of the Bükk National Park Directorate (light brown), Bükk National Park areas (green) and camera trap locations (orange).

Camera-traps, together with the buffer zone, covered a 197 km<sup>2</sup> polygone, but probably this is the most frequently visited site by wolves within the whole NPD (Gombkötő, pers. comm.). Thus, I used this value when calculated the REM density and it is not possible to interpolate these data for the whole area, although probably the wolf density would be similar in both the NP and the NPD.

In the case of the genetic study (Stéger, 2019) there is no area given, thus it is not possible to calculate a proper density. Also, even this study was biased by opportunistic sample collecting throughout the NPD. Most scat was collected in places where national park employees knew that wolves are present (eg. they avoided searching for samples near settlements or lowland areas).

Theoretically, density results should be comparable (e.g. in the Yucon there are 1.2 wolf individuals/100 km<sup>2</sup> (Hayes and Harestad 2000) while it is 1.36 individuals per 100 km<sup>2</sup> in the Denali National Park (Burch et al. 2005)). As in my case there is no certain area, it is not possible to compare it to international values. To be able to calculate a comparable value, radiotelemetry studies should complete my analysis to be sure about the exact area that the species use daily.

There is another possible bias incorporated in my study due to the current level of general knowledge about the Hungarian wolves. We do not have the necessary and concrete basic data yet (e.g. daily movement speed of the wolf), hence data from Poland (Jedrzejewski et al. 2001) was used to refine our model.

Also, for more reliable REM estimations cameras' technical details should be considered. Rowcliffe (2018) himself suggests calculating camera characteristics ( $\Theta$  and  $r$ ) to every camera of the study instead of using the manual as those values are usually much smaller on field localities due to the surrounding environment or sometimes weather conditions. Caravaggi et al. (2016) demonstrated a reference grid, photographed with each camera of concern in the beginning of the study, and the reference grid was underlaid to each further photo the camera taken with 50% transparency and correct distance values were calculated trigonometrically.

This way, camera hours can be tested as well instead of camera days: unfortunately, it is not coherent in the literature what does one consider for survey effort. Some articles calculate with camera hours (e.g. Caravaggi et al. 2016, Caravaggi et al. 2017) and some with camera days (e.g. Balestrieri et al. 2016, Popova et al. 2018). Although it makes sense to assign our choice with how the travel speed was defined in the reference article (i.e. km/day or km/24 hours) – the travel speed itself is the same both cases as 24 hours is equal to a day. Seemingly, it was just a matter of choice how our reference articles defined the travel speed – however, it seems how we define survey effort really does influence the final REM estimation. For example, in my case, camera days were used, following Popova et al (2018). Camera days were equal to 591, 793 and 670 (2016-2017-2018, respectively) which would be 14184, 19032 and 16080 hours, respectively. That would drastically reduce the estimation, for example in 2016 it would mean 0.6 individual for 197 km<sup>2</sup> instead of 15.6.

Current population estimations in Hungary for large mammals are based on annual harvest bags (game species) or occasional genetic analysis (protected large carnivores). The former, however, is not quite reliable (Szemethy 2020), while the latter can be time- and money consuming (Long et al. 2008) and according to some literatures, not necessarily non-invasive (Brzeziński and Romanowski 2006). As I was able to produce similar wolf population density estimations as the DNA based reference densities, I recommend REM to be part of the general toolkit of wildlife management in Hungary, however a serious improvement of the study design is necessary if NP rangers or wildlife managers would like to complement or improve the current monitoring methods with REM, especially for large carnivore species and ungulates.

To get reliable results, REM field design must be more of a concern. First of all, at least 20 cameras are needed per site, operating for at least 500 camera days and with minimum 20 independent registrations for the species in study (Rowcliffe et al. 2008). Positions of camera traps should be fix and not relocated too often, also there must be regular check-ups for the cameras to avoid weeks out of order. National Park staff installed the cameras opportunistically in order to capture wolf images and get a better understanding of their movement within the park, however as years went by, they used more cameras in areas and routes where wolf movement were previously proved. This means that my survey was based on fewer cameras than suggested by the model (but I still used all the cameras that were



available in the park) and which were (i) opportunistically (ii) and non-randomly placed while (iii) sometimes were reinstalled to other locations that resulted in unequal sampling units. Despite the fact that my population estimation data align with reference densities, unequally and randomly sampled sites might cause bias (Cusack et al. 2015; Rowcliffe et al. 2008) and it is highly recommended for further testing the REM and to find fix locations and random study design in the future and stick to that even if the camera stock is improving during the years.

Until then, using REM next to the other current methods (e.g. genetics, driven hunt census) can lead to more reliable population estimations and can cross-check each method biases. Using several estimation methods simultaneously is commonly carried out in wildlife management (e.g. for wolverine Magoun et al. (2011) used hairsnags and camera traps, for wolf Roffler et al. (2016) used radio tracking, trail cameras and different counts, while Kojola et al. (2014) used track survey, reproduction survey and the Finnish triangle method).

Camera traps have already been proved to be an effective and relatively cheap way of non-invasive and long-term monitoring (Long et al. 2008). In case of elusive, protected species it is probably one of the best way to study their normal behaviour including their use of time, as an ecological resource, like in the case of activity patterns and activity overlap studies or studying their population dynamics, like in case of the Random Encounter Model.

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## Chapter 4 - Final remarks

In my thesis I made a novel attempts (REM and activity overlap) in Hungary to use camera-trap data to assess the dynamics of the relationship between the naturally returning wolf and its prey (red deer, roe deer, wild boar) and competitor (red fox) species. The methods I used are well researched (Ridout and Linkie, 2009; Brown et al. 2001; Foster et al. 2013; Rowcliffe et al. 2008; Caravaggi et al. 2016, Caravaggi et al. 2017; Balestrieri et al. 2016, Popova et al. 2018) but they are still not widely used in Eastern-Europe, especially not in the Carpathian basin. As the Hungarian literature on wolf ecology and monitoring methods are very scarce, my results can contribute to the development wildlife and game management methods, which are more effective and less expensive for Hungarian professionals.

Wildlife practitioners (e.g. hunters, livestockbreeders) often complain that the expanding wolf population not only predate, but simply by their presence, disturbs the normal behaviour of ungulates that makes hunting complicated (Højberg et al. 2017; Patkó, pers comm.). According to my results, ungulates did not show any sign of temporal segregation, as overlap coefficients were generally high (the highest was red deer:  $\Delta=0.87$ ; lowest was roe deer:  $\Delta=0.79$ ). This means the species co-exist at the same time within the same area, thus prey species probably need to use more sophisticated behaviours in order to avoid an encounter with the wolf. However, in critical periods of the year, such as rutting (roe deer:  $\Delta=0.64$ ) or birthing (wild boar:  $\Delta=0.5$ ), these observations might be temporarily true. As these values are still above  $\Delta=0.5$ , hunters concern on how wolf's presence disturb ungulates is not completely confirmed, as the lack of temporal segregation likely contribute to possible encounters after all.

Non-invasive camera traps are handful tools for wildlife management as they are relatively cheap, durable and make constant, long-term monitoring possible while not disturbing the normal behaviour of the target species – however it is still not part of the general toolkit of Hungarian game wardens and National Park (NP) rangers. In this thesis I tested a statistical method that makes population density estimations possible without the individual recognition of the animals, called the Random Encounter Model (REM). When estimating the wolf population with REM I was able to get similar results as the reference densities (wolf:  $\bar{n}=16$

individuals;  $\overline{SD}$  = 1.28 individuals; reference density:  $STR_{n=14}$  ind. (Stéger 2019)) but the testing clearly revealed that there are critical constraints of the model that must be taken into consideration in the future study design. First of all, at least 20 cameras are needed per site, operating for at least 500 camera days and with minimum 20 independent registrations for the species in study (Rowcliffe et al. 2008). Positions of camera traps should be fix and not relocated too often, also there must be regular check-ups for the cameras to avoid weeks out of order. But the most important lesson is that the field design should prevent both avoiding and targeting the focal species.

National Parks should insist on further testings of camera-based behavioural and populational studies for which they should install a stable camera stock that focuses on long-term studies, thus camera sites are not changed through the years.

Game managers are encouraged to start including camera traps in their protocols and share their data with NPs to contribute to the currently poor datapool about large carnivores relationship with wild ungulates. For the same reason, Hungarian scientists and conservationists should improve the general basic information on these animals, like the daily movement data that is required to refine the REM. Since these stakeholder groups use the same natural resources (wildlife) with similar techniques their data should be shared with each other.

There is another novel statistical method, called REST, which is the extension of the REM and which uses video footage and accounts for the staying time instead of the daily movement speed of animals (Nakashima et al., 2018). The model describes the relationship between trapping time, detection rate and population density. It is vulnerable to unsynchronized activity patterns among individuals but has better efficiency and higher feasibility than REM regardless (Nakashima et al. 2018).

The exact estimation of activity patterns is important when doing REST studies thus the results of my thesis can contribute to a third, more accurate measure to describe predator-prey relationships in the Hungarian mid-mountains.

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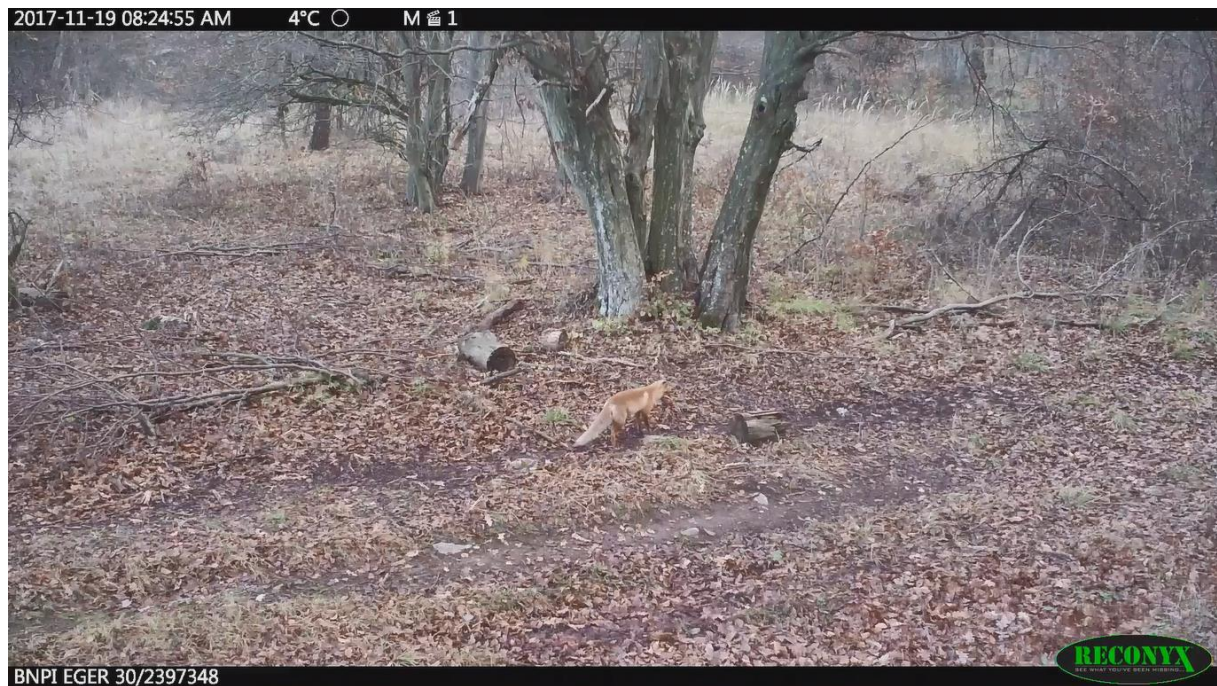
# Appendix

- I. Daytime and nighttime example of photos taken by camera traps (Reconyx UltraFire XR6; HyperFire HC500, PC900 and PC800; RapidFire PM75) in Bükk National Park, Hungary.



**Appendix I/1.** Daytime picture of a red deer taken by Reconyx HC500 HYPERFIRE.





**Appendix I/2.** Daytime picture of a red fox taken by Reconyx PC900.

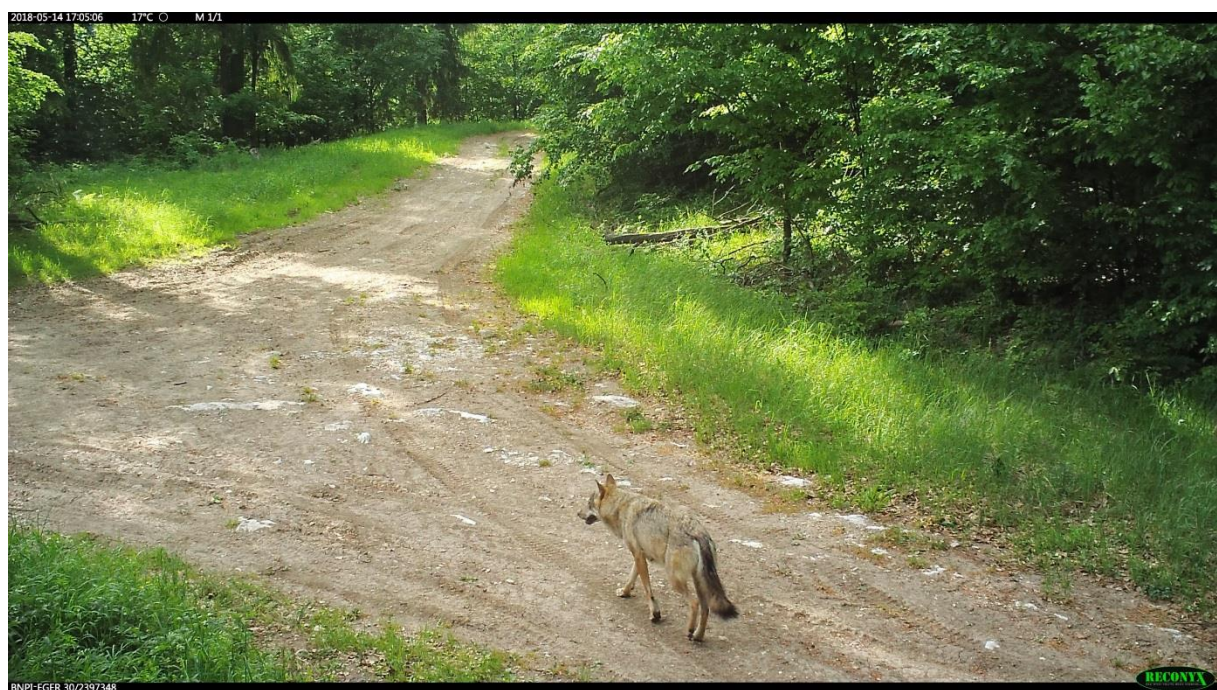


**Appendix I/3.** Nighttime picture of a roe deer taken by Reconyx HC500 HYPERFIRE.





**Appendix I/4.** Daytime picture of a wild boar and a piglet taken by Reconyx PC900.



**Appendix I/5.** Daytime picture of a grey wolf taken by Reconyx PC900.



## II. Field work.



**Appendix II/1.** Checking camera traps in Bükk National Park with Péter Gombkötő (BNPD).



**Appendix II/2.** Checking camera traps in Bükk National Park with Péter Gombkötő (BNPD) and László Patkó (WWF Hungary).



### III. Samples of original datasheets.

A

	A	B	C	D	E	F	G	H	I	J	K
1	Site	Year	Date	Start	Species	Quant	Male	Female	Young	Notes	Camera
198	Csigaret	2016	2016.01.14	18:08:10	indet	1				szerintem.roka	RECONYX.HC500.HYPERFIRE
199	Csigaret	2016	2016.01.16	2:28:31	indet	1					RECONYX.HC500.HYPERFIRE
200	Csigaret	2016	2016.01.18	6:01:10	indet	1					RECONYX.HC500.HYPERFIRE
201	Csigaret	2016	2016.01.18	15:32:17	VULVUL	1					RECONYX.HC500.HYPERFIRE
202	Csigaret	2016	2016.01.19	15:47:20	VULVUL	1					RECONYX.HC500.HYPERFIRE
203	Csigaret	2016	2016.01.24	13:09:52	VULVUL	1					RECONYX.HC500.HYPERFIRE
204	Csigaret	2016	2016.01.26	16:42:25	SUSSCR	9				IMG_0335	RECONYX.HC500.HYPERFIRE
205	csigarét	2016	2016.01.14	18:08:10	indet	1					RECONYX.HC500.HYPERFIRE
206	csigarét	2016	2016.01.16	2:28:31	indet	1					RECONYX.HC500.HYPERFIRE
207	csigarét	2016	2016.01.18	6:01:10	indet	1					RECONYX.HC500.HYPERFIRE
208	csigarét	2016	2016.01.18	15:32:17	VULVUL	1					RECONYX.HC500.HYPERFIRE
209	csigarét	2016	2016.01.18	19:04:55	indet	1					RECONYX.HC500.HYPERFIRE
210	csigarét	2016	2016.01.19	15:47:20	VULVUL	1					RECONYX.HC500.HYPERFIRE
211	csigarét	2016	2016.01.24	13:09:52	VULVUL	1					RECONYX.HC500.HYPERFIRE
212	csigarét	2016	2016.01.26	16:42:25	SUSSCR	9			6	maybe.more	RECONYX.HC500.HYPERFIRE
213	csigarét	2016	2016.02.02	7:38:35	CANLUP	1					RECONYX.HC500.HYPERFIRE
214	csigarét	2016	2016.02.03	12:29:40	CAPCAP	2		1		leg.on.the.left	RECONYX.HC500.HYPERFIRE
215	csigarét	2016	2016.02.08	3:37:54	VULVUL	1					RECONYX.HC500.HYPERFIRE
216	csigarét	2016	2016.02.09	20:50:27	indet	1					RECONYX.HC500.HYPERFIRE
217	csigarét	2016	2016.02.17	17:01:09	VULVUL	1				marking.territory	RECONYX.HC500.HYPERFIRE
218	csigarét	2016	2016.02.17	17:59:51	VULVUL	1					RECONYX.HC500.HYPERFIRE
219	csigarét	2016	2016.02.18	16:57:39	CERELA	2		2			RECONYX.HC500.HYPERFIRE
220	csigarét	2016	2016.02.19	0:25:03	indet	1					RECONYX.HC500.HYPERFIRE
221	csigarét	2016	2016.02.25	11:45:46	VULVUL	1				individual.count	RECONYX.HC500.HYPERFIRE
222	csigarét	2016	2016.03.01	1:58:47	indet	1					RECONYX.HC500.HYPERFIRE
223	csigarét	2016	2016.03.14	19:26:40	indet	1					RECONYX.HC500.HYPERFIRE
224	csigarét	2016	2016.03.18	15:32:19	VULVUL	1					RECONYX.HC500.HYPERFIRE

Appendix III/1. Original raw Excel datasheet (total record of 4292).

# B

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
1	Site	Year	Date	Start	Hour	Minute	Second	TotalSec	SecondIn	TimeRad	Species	Male	Female	Young
2	1	2016	2016.01.26	16:42:25	16	42	25	60145	0,69612	4,37374	SUSSCR	NA	NA	NA
3	1	2016	2016.02.02	7:38:35	7	38	35	27515	0,31846	2,00089	CANLUP	NA	NA	NA
4	1	2016	2016.04.01	5:24:40	5	24	40	19480	0,22546	1,41658	CANLUP	NA	NA	NA
5	1	2016	2016.05.03	19:17:35	19	17	35	69455	0,80388	5,05076	CANLUP	NA	NA	NA
6	2	2016	2016.05.04	4:11:58	4	11	58	15118	0,17498	1,09938	CANLUP	NA	NA	NA
7	1	2017	2017.02.09	17:43:03	17	43	3	63783	0,73823	4,63829	SUSSCR	NA	NA	NA
8	1	2017	2017.02.09	18:35:10	18	35	10	66910	0,77442	4,86569	SUSSCR	NA	1	8
9	1	2017	2017.02.21	11:03:48	11	3	48	39828	0,46097	2,89629	CAPCAP	NA	NA	NA
10	1	2017	2017.02.26	20:33:55	20	33	55	74035	0,85689	5,38382	SUSSCR	NA	NA	NA
11	1	2017	2017.02.27	8:37:28	8	37	28	31048	0,35935	2,25781	CAPCAP	NA	NA	NA
12	1	2017	2017.03.01	3:43:16	3	43	16	13396	0,15505	0,97416	CAPCAP	NA	NA	NA
13	1	2017	2017.03.04	0:48:19	0	48	19	2899	0,03355	0,21082	SUSSCR	NA	NA	NA
14	1	2017	2017.03.04	19:24:13	19	24	13	69853	0,80848	5,0797	CERELA	1	NA	NA
15	1	2017	2017.03.08	18:39:23	18	39	23	67163	0,77735	4,88409	CAPCAP	NA	NA	NA
16	1	2017	2017.03.10	7:06:48	7	6	48	25608	0,29639	1,86221	CERELA	NA	1	NA
17	1	2017	2017.03.10	23:04:18	23	4	18	83058	0,96132	6,03997	SUSSCR	NA	1	6
18	1	2017	2017.03.14	19:12:39	19	12	39	69159	0,80045	5,02924	SUSSCR	NA	NA	NA
19	1	2017	2017.03.18	3:26:07	3	26	7	12367	0,14314	0,89933	SUSSCR	NA	NA	NA
20	1	2017	2017.03.20	16:22:40	16	22	40	58960	0,68241	4,28757	CAPCAP	NA	NA	NA
21	1	2017	2017.03.20	23:41:16	23	41	16	85276	0,98699	6,20126	SUSSCR	NA	NA	NA
22	1	2017	2017.03.23	8:04:56	8	4	56	29096	0,33676	2,11586	SUSSCR	NA	NA	NA
23	1	2017	2017.03.24	5:58:51	5	58	51	21531	0,2492	1,56573	SUSSCR	NA	NA	2
24	1	2017	2017.03.26	14:22:35	14	22	35	51755	0,59902	3,76362	CERELA	1	4	NA
25	1	2017	2017.03.27	17:20:22	17	20	22	62422	0,72248	4,53932	CERELA	1	1	NA
26	1	2017	2017.03.28	2:45:46	2	45	46	9946	0,11512	0,72327	SUSSCR	NA	NA	NA
27	1	2017	2017.03.28	5:43:43	5	43	43	20623	0,23869	1,4997	SUSSCR	NA	NA	6
28	1	2017	2017.03.30	20:01:43	20	1	43	72103	0,83453	5,24332	SUSSCR	NA	1	1

**Appendix III/2.** Transformed datasheet for activity overlap calculation.

# C

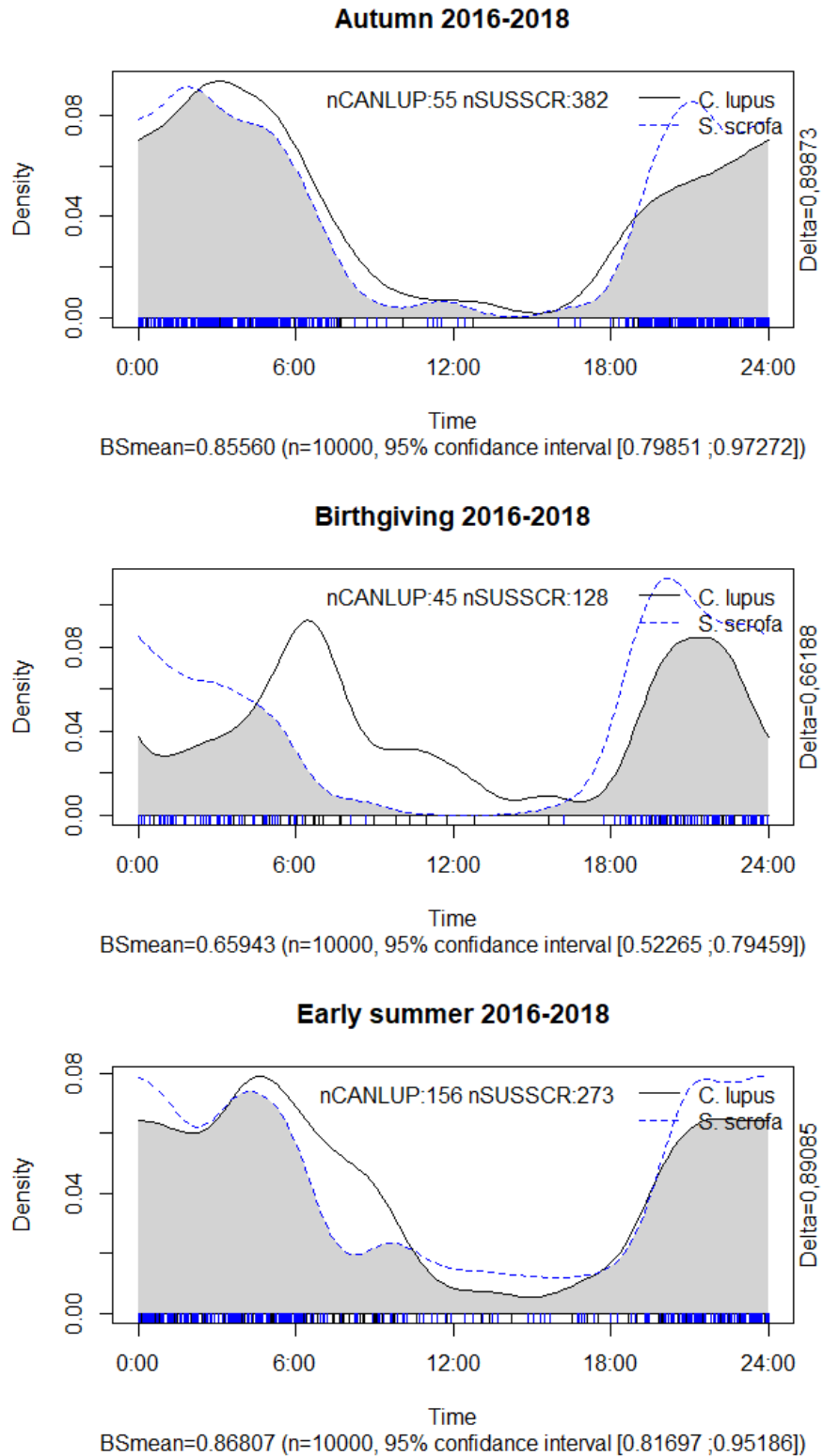
	A	B	C	D
1	Site	Count	Dist	Theta
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3	1	1	0,03	0,698
4	1	1	0,03	0,698
5	1	1	0,03	0,698
6	1	1	0,03	0,698
7	1	1	0,03	0,698
8	1	2	0,03	0,698
9	1	1	0,03	0,698
10	1	1	0,03	0,698
11	1	1	0,03	0,698
12	1	2	0,03	0,698
13	1	1	0,03	0,698
14	1	1	0,03	0,698
15	1	1	0,03	0,698
16	1	3	0,03	0,698
17	1	1	0,03	0,698
18	1	1	0,03	0,698
19	1	1	0,03	0,698
20	1	3	0,03	0,698
21	1	1	0,03	0,698
22	1	1	0,03	0,698
23	1	1	0,03	0,698
24	1	3	0,03	0,698
25	1	2	0,03	0,698
26	1	1	0,03	0,698
27	1	1	0,03	0,698
28	1	1	0,03	0,698

**Appendix III/3.**

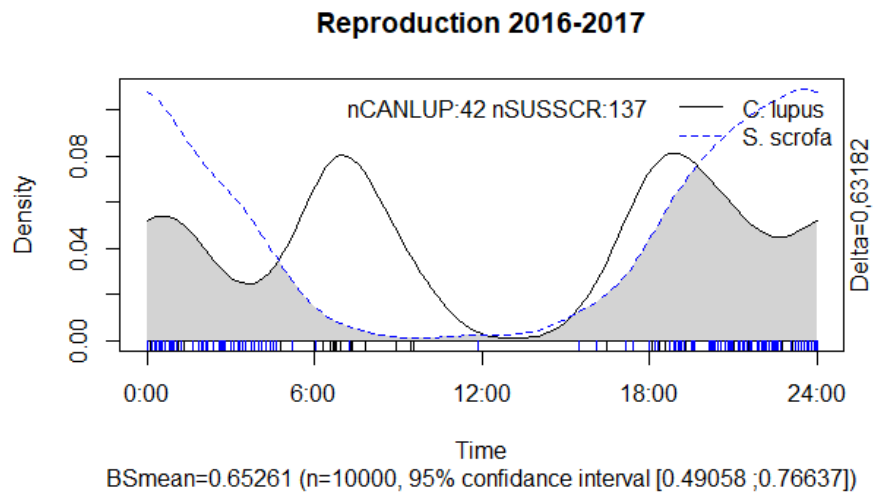
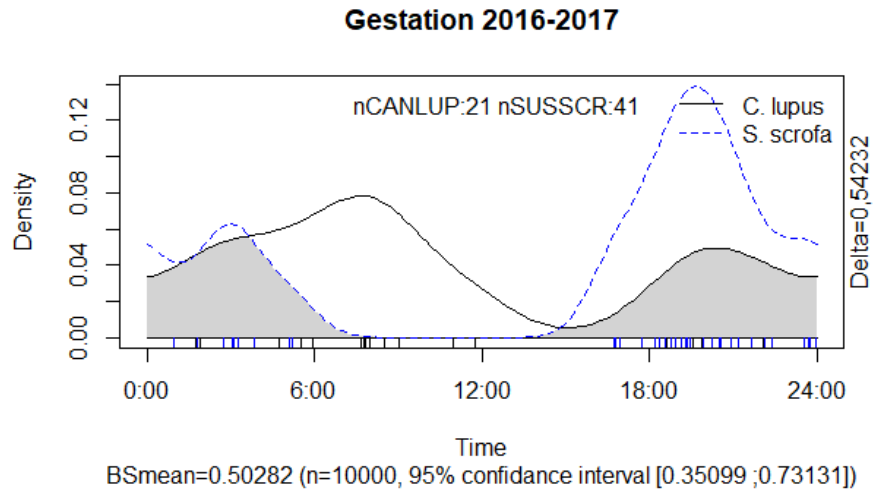
Transformed datasheet for the Random Encounter Modell (REM).

#### IV. Activity overlaps

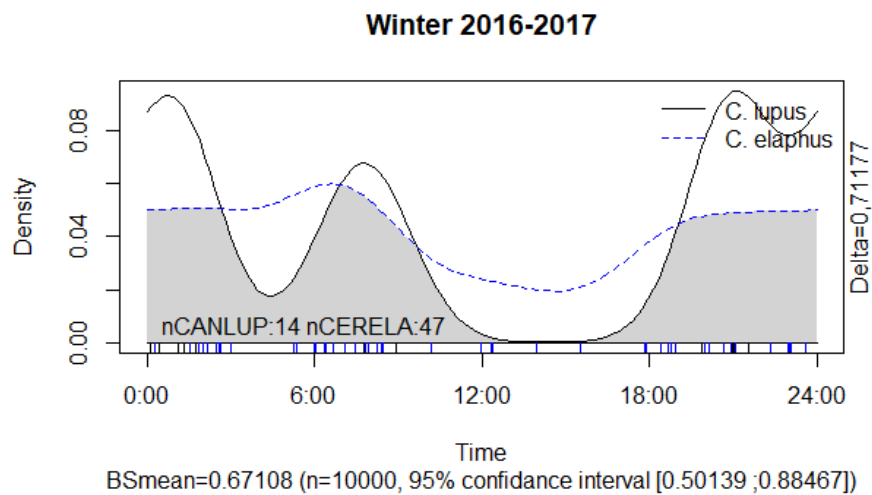
A) Example for how activity overlaps change through seasons between wolf (*C. lupus*) and wild boar (*S. Scrofa*) in Bükk National Park, Hungary (2016-2018).

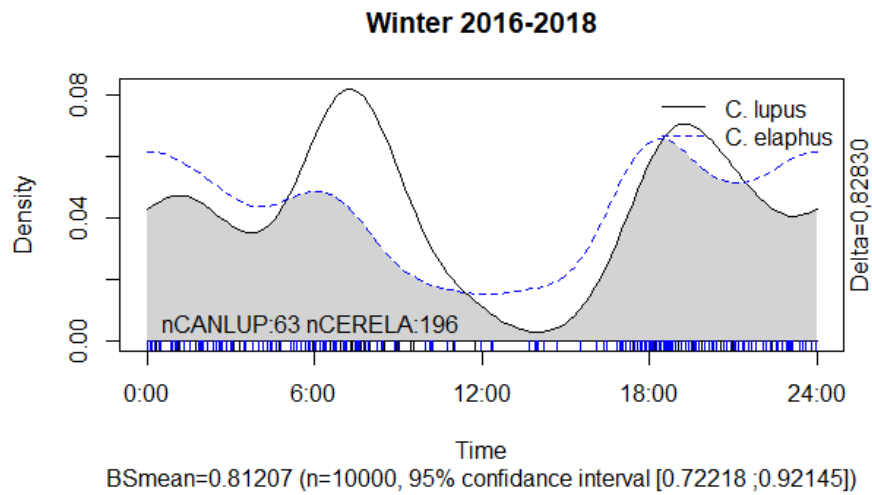
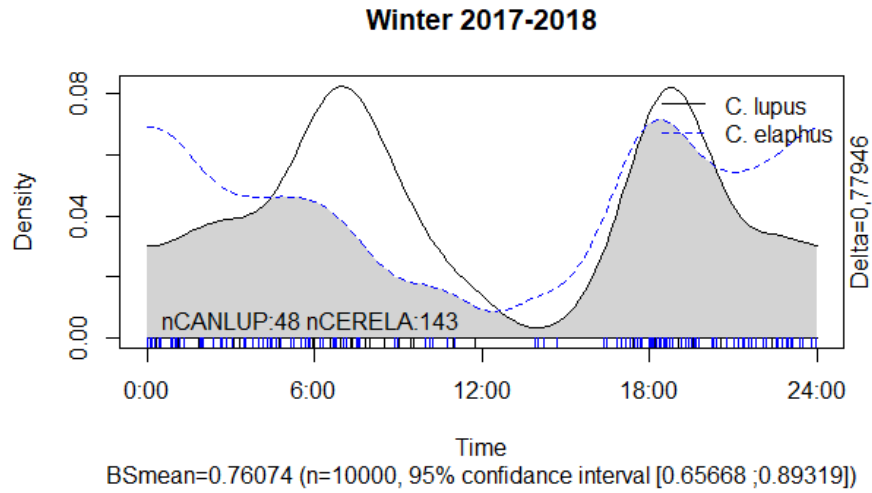




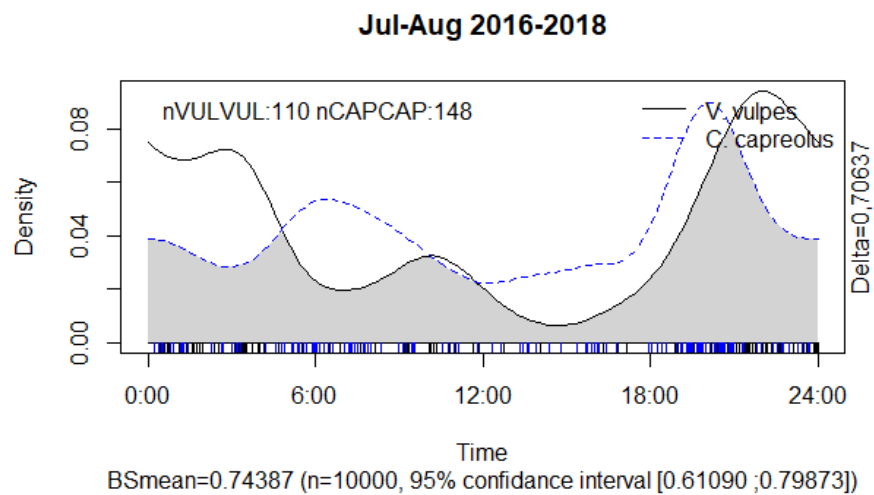


- B) Example for how activity overlaps change through years between wolf (*C. lupus*) and red deer (*C. elaphus*) in Bükk National Park, Hungary (2016-2018). (Winter season was defined as November-December-January-February)

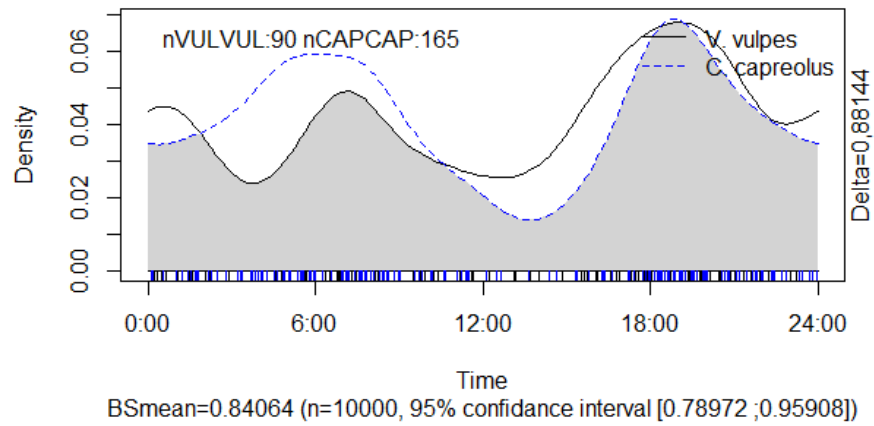




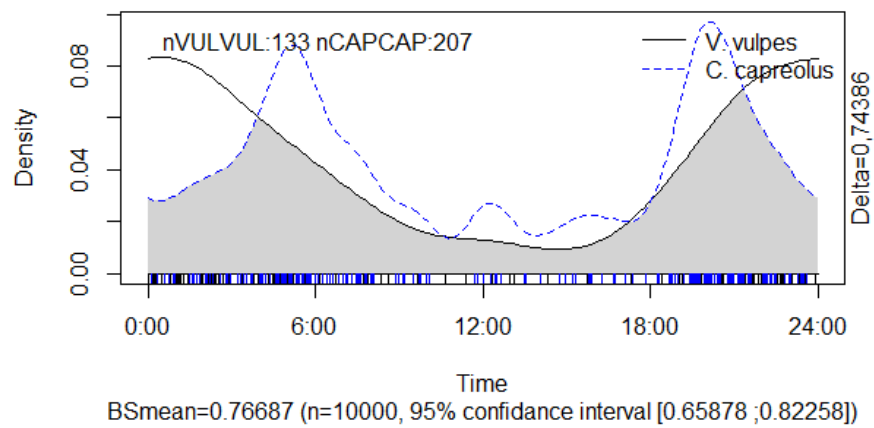
C) Example for a fox (*V. Vulpes*) and roe deer (*C. capreolus*) analysis throughout different seasons.



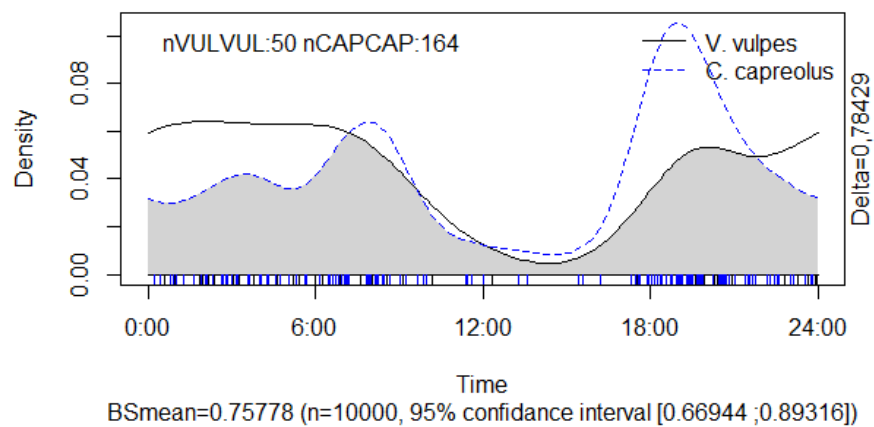
### March-April 2016-2018



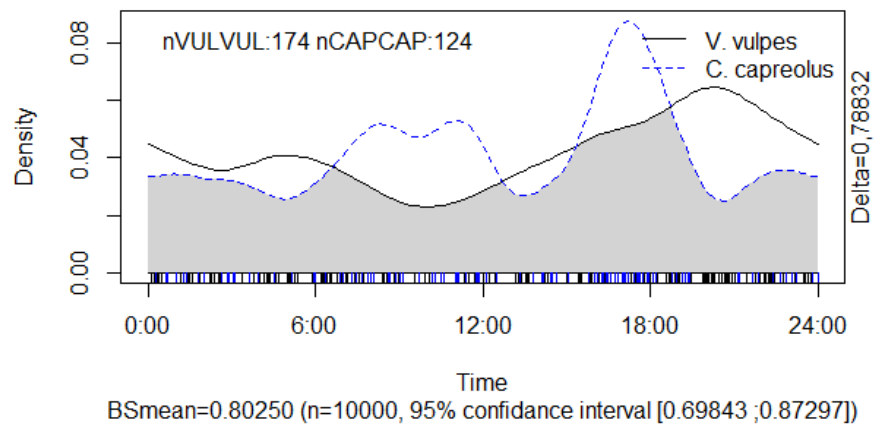
### May-Jun 2016-2018



### Sept-Oct 2016-2018



### Winter 2016-2018



## V. R Scripts

### A) Activity overlap (R package: overlap)

```
table(X2016_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!
```

```
TimeRad=X2016_tavasz$Secondln * 2 * pi
#caution for changing the source file!
```

```
wolf <- TimeRad[X2016_tavasz$Species == 'CANLUP']
boar <- TimeRad[X2016_tavasz$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat1")
wolboarest
overlapPlot(wolf, boar, main="Pup ubringing 2016", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,74817", side=4)
corner_text(text="nCANLUP:27 nSUSSCR:46",location= "topleft")
```

```
wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval
```

```
bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0
```

```
title(sub="BSmean=0.70661 (n=10000, 95% confidence interval [0.56627 ;0.90207])")
```

```
#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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```

```
table(X2017_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!
```

```
TimeRad=X2017_tavasz$Secondln * 2 * pi
#caution for changing the source file!
```

```
wolf <- TimeRad[X2017_tavasz$Species == 'CANLUP']
boar <- TimeRad[X2017_tavasz$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat1")
wolboarest
overlapPlot(wolf, boar, main="Pup ubringing 2017", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,69409", side=4)
corner_text(text="nCANLUP:28 nSUSSCR:40",location= "topleft")
```

```
wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval
```

```
bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0
```

```
title(sub="BSmean=0.67459 (n=10000, 95% confidence interval [0.50885 ;0.86116])")
```

```

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(X2018_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2018_tavasz$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2018_tavasz$Species == 'CANLUP']
boar <- TimeRad[X2018_tavasz$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Pup ubringing 2018", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,83806", side=4)
corner_text(text="nCANLUP:84 nSUSSCR:92",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.81311 (n=10000, 95% confidance interval [0.73133 ;0.93297])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(X2016_2018_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2016_2018_tavasz$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2016_2018_tavasz$Species == 'CANLUP']
boar <- TimeRad[X2016_2018_tavasz$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Pup ubringing 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,82090", side=4)
corner_text(text="nCANLUP:139 nSUSSCR:178",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.81407 (n=10000, 95% confidance interval [0.73599 ;0.89930])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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```

```
table(X2018_tavaszs$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!
```

```
TimeRad=X2018_tavaszi$Secondln * 2 * pi
#caution for changing the source file!
```

```
wolf <- TimeRad[X2018_tavasz$Species == 'CANLUP']
boar <- TimeRad[X2018_tavasz$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Pup ubringing 2018", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,83806", side=4)
corner text(text="nCANLUP:84 nSUSSCR:92",location= "topleft")
```

```
wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval
```

```
bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0
```

```
title(sub="BSmean=0.81311 (n=10000, 95% confidence interval [0.73133 ;0.93297])")
```

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE  
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NDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEEND

```
table(X2016_2018_tavaszs$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!
```

```
TimeRad=X2016_2018_tavasz$Secondln * 2 * pi
#caution for changing the source file!
```

```
wolf <- TimeRad[X2016_2018_tavaszs$Species == 'CANLUP']
boar <- TimeRad[X2016_2018_tavaszs$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Pup ubringing 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,82090", side=4)
corner text(text="nCANLUP:139 nSUSSCR:178",location= "topleft")
```

```
wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval
```

```
bootCI(wolboarest, wolfoar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0
```

```
title(sub="BSmean=0.81407 (n=10000, 95% confidence interval [0.73599 ;0.89930])")
```

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE  
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NDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEEND



```

TimeRad=X2017_2018_tel$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2017_2018_tel$Species == 'CANLUP']
boar <- TimeRad[X2017_2018_tel$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat1")
wolboarest
overlapPlot(wolf, boar, main="Winter 2017-2018", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,55297", side=4)
corner_text(text="nCANLUP:48 nSUSSCR:112",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.56274 (n=10000, 95% confidance interval [0.42400 ;0.67860])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
NDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(tel_total$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=tel_total$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[tel_total$Species == 'CANLUP']
boar <- TimeRad[tel_total$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Winter 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "S.Scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,64833", side=4)
corner_text(text="nCANLUP:63 nSUSSCR:178",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.65448 (n=10000, 95% confidance interval [0.53182 ;0.75880])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(X2016_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2016_tavasz$Secondln * 2 * pi
#caution for changing the source file!

```





```

wolcapcapest<- overlapEst(wolf, capcap, type="Dhat4")
wolcapcapest
overlapPlot(wolf, capcap, main="Pup ubringing 2018", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,78450", side=4)
corner_text(text="nCANLUP:84 nCAPCAP:91",location= "bottomleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.77928 (n=10000, 95% confidence interval [0.67852 ;0.88250])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(X2016_2018_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2016_2018_tavasz$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2016_2018_tavasz$Species == 'CANLUP']
capcap <- TimeRad[X2016_2018_tavasz$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolcapcapest<- overlapEst(wolf, capcap, type="Dhat4")
wolcapcapest
overlapPlot(wolf, capcap, main="Pup ubringing 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,80334", side=4)
corner_text(text="nCANLUP:139 nCAPCAP:312",location= "bottomleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.81165 (n=10000, 95% confidence interval [0.72931 ;0.87119])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
NDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
NDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE

table(X2016_2017_tel$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2016_2017_tel$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2016_2017_tel$Species == 'CANLUP']
capcap <- TimeRad[X2016_2017_tel$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolcapcapest<- overlapEst(wolf, capcap, type="Dhat1")
wolcapcapest
overlapPlot(wolf, capcap, main="Winter 2016-2017", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')

```



```

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolfcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.72144 (n=10000, 95% confidence interval [0.60310 ;0.81156])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
NTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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NTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE

table(uzekedes_2016$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=uzekedes_2016$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[uzekedes_2016$Species == 'CANLUP']
capcap <- TimeRad[uzekedes_2016$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolfcapcapest<- overlapEst(wolf, capcap, type="Dhat1")
wolfcapcapest
overlapPlot(wolf, capcap, main="Rut 2016", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,36419", side=4)
corner_text(text="nCANLUP:10 nCAPCAP:33",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolfcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.37737 (n=10000, 95% confidence interval [0.14991 ;0.58548])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
NTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
NTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE

table(uzekedes_2017$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=uzekedes_2017$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[uzekedes_2017$Species == 'CANLUP']
capcap <- TimeRad[uzekedes_2017$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolfcapcapest<- overlapEst(wolf, capcap, type="Dhat1")
wolfcapcapest
overlapPlot(wolf, capcap, main="Rut 2017", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,56689", side=4)
corner_text(text="nCANLUP:22 nCAPCAP:93",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)

```

```

wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.56719 (n=10000, 95% confidence interval [0.42481 ;0.70966])")

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table(uzekedes_2018$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=uzekedes_2018$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[uzekedes_2018$Species == 'CANLUP']
capcap <- TimeRad[uzekedes_2018$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolcapcapest<- overlapEst(wolf, capcap, type="Dhat1")
wolcapcapest
overlapPlot(wolf, capcap, main="Rut 2018", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,83628", side=4)
corner_text(text="nCANLUP:19 nCAPCAP:22",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.70343 (n=10000, 95% confidence interval [0.63510 ;0.99728])")

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table(uzekedes_total$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=uzekedes_total$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[uzekedes_total$Species == 'CANLUP']
capcap <- TimeRad[uzekedes_total$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolcapcapest<- overlapEst(wolf, capcap, type="Dhat4")
wolcapcapest
overlapPlot(wolf, capcap, main="Rut 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,61858", side=4)
corner_text(text="nCANLUP:51 nCAPCAP:148",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

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bootCI(wolcapcapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.63769 (n=10000, 95% confidence interval [0.50129 ;0.73318])")

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table(X2016_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2016_tavasz$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2016_tavasz$Species == 'CANLUP']
cerela <- TimeRad[X2016_tavasz$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat1")
wolcerelaest
overlapPlot(wolf, cerela, main="Pup ubreeding 2016", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,76085", side=4)
corner_text(text="nCANLUP:27 nCERELA:127",location= "topleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.72551 (n=10000, 95% confidence interval [0.62152 ;0.88347])")

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table(X2017_tavasz$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=X2017_tavasz$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[X2017_tavasz$Species == 'CANLUP']
cerela <- TimeRad[X2017_tavasz$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat1")
wolcerelaest
overlapPlot(wolf, cerela, main="Pup ubreeding 2017", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,81179", side=4)
corner_text(text="nCANLUP:28 nCERELA:103",location= "bottomleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:

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table(tel_total$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=tel_total$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[tel_total$Species == 'CANLUP']
cerela <- TimeRad[tel_total$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat4")
wolcerelaest
overlapPlot(wolf, cerela, main="Winter 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,82830", side=4)
corner_text(text="nCANLUP:63 nCERELA:196",location= "bottomleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.81207 (n=10000, 95% confidence interval [0.72218 ;0.92145])")

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table(boges_2016$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=boges_2016$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[boges_2016$Species == 'CANLUP']
cerela <- TimeRad[boges_2016$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat1")
wolcerelaest
overlapPlot(wolf, cerela, main="Rut 2016", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,71354", side=4)
corner_text(text="nCANLUP:10 nCERELA:153",location= "bottomleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.61988 (n=10000, 95% confidence interval [0.49229 ;0.91819])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(boges_2017$Species)

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#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=boges_2017$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[boges_2017$Species == 'CANLUP']
cerela <- TimeRad[boges_2017$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat1")
wolcerelaest
overlapPlot(wolf, cerela, main="Rut 2017", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,79498", side=4)
corner_text(text="nCANLUP:30 nCERELA:109",location= "top")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.77050 (n=10000, 95% confidence interval [0.64012 ;0.92193])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(boges_total$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=boges_total$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[boges_total$Species == 'CANLUP']
cerela <- TimeRad[boges_total$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat4")
wolcerelaest
overlapPlot(wolf, cerela, main="Rut 2016-2017", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,81092", side=4)
corner_text(text="nCANLUP:52 nCERELA:278",location= "top")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.79443 (n=10000, 95% confidence interval [0.69537 ;0.91614])")

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table(preboges_2016$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

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[illegible]

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cerela <- TimeRad[preboges_2018$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat1")
wolcerelaest
overlapPlot(wolf, cerela, main="Pre-rut 2018", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,81221", side=4)
corner_text(text="nCANLUP:19 nCERELA:41",location= "top")


wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval


bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0


title(sub="BSmean=0.72932 (n=10000, 95% confidence interval [0.62430 ;0.96492])")


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table(preboges_total$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!


TimeRad=preboges_total$Secondln * 2 * pi
#caution for changing the source file!


wolf <- TimeRad[preboges_total$Species == 'CANLUP']
cerela <- TimeRad[preboges_total$Species == 'CERELA']
min(length(wolf), length(cerela))
wolcerelaest<- overlapEst(wolf, cerela, type="Dhat4")
wolcerelaest
overlapPlot(wolf, cerela, main="Pre-rut 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,83264", side=4)
Corner_text(text="nCANLUP:51 nCERELA:307",location= "top")


wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval


bootCI(wolcerelaest, wolfcerela2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0


title(sub="BSmean=0.80397 (n=10000, 95% confidence interval [0.72723 ;0.92080])")


#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(elles$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!


TimeRad=elles$Secondln * 2 * pi
#caution for changing the source file!


wolf <- TimeRad[elles$Species == 'CANLUP']
boar <- TimeRad[elles$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat1")
wolboarest
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overlapPlot(wolf, boar, main="Birthgiving 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "S. scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,66188", side=4)
Corner_text(text="nCANLUP:45 nSUSSCR:128",location= "top")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.65943 (n=10000, 95% confidance interval [0.52265 ;0.79459])")

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table(nyar$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=nyar$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[nyar$Species == 'CANLUP']
boar <- TimeRad[nyar$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Early summer 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "S. scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,89085", side=4)
Corner_text(text="nCANLUP:156 nSUSSCR:273",location= "top")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
boarboot <- resample(boar, 10000)
dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.86807 (n=10000, 95% confidance interval [0.81697 ;0.95186])")

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table(maganyoshimek$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=maganyoshimek$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[maganyoshimek$Species == 'CANLUP']
boar <- TimeRad[maganyoshimek$Species == 'SUSSCR']
min(length(wolf), length(boar))
wolboarest<- overlapEst(wolf, boar, type="Dhat4")
wolboarest
overlapPlot(wolf, boar, main="Autumn 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "S. scrofa"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,89873", side=4)
Corner_text(text="nCANLUP:55 nSUSSCR:382",location= "top")

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dim(boarboot)
wolfboar2 <- bootEst(wolfboot, boarboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.50282 (n=10000, 95% confidence interval [0.35099 ;0.73131])")

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table(ozelles$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=ozelles$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[ozelles$Species == 'CANLUP']
capcap <- TimeRad[ozelles$Species == 'CAPCAP']
min(length(wolf), length(capcap))
wolcapapest<- overlapEst(wolf, capcap, type="Dhat4")
wolcapapest
overlapPlot(wolf, capcap, main="Birthgiving 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,77362", side=4)
Corner_text(text="nCANLUP:120 nCAPCAP:207",location= "bottomleft")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
wolfcapcap2 <- bootEst(wolfboot, capcapboot, type="Dhat4")
( BSmean <- mean(wolfcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolcapapest, wolfcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.78931 (n=10000, 95% confidence interval [0.68709 ;0.85235])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(szarvaselles$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=szarvaselles$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[szarvaselles$Species == 'CANLUP']
cerela <- TimeRad[szarvaselles$Species == 'CERELA']
min(length(wolf), length(cerela))
wolverelaest<- overlapEst(wolf, cerela, type="Dhat4")
wolverelaest
overlapPlot(wolf, cerela, main="Birthgiving 2016-2018", rug = TRUE)
legend('topright', c("C. lupus", "C. elaphus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,75317", side=4)
Corner_text(text="nCANLUP:51 nCERELA:160",location= "top")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
cerelaboot <- resample(cerela, 10000)
dim(cerelaboot)
wolfcerela2 <- bootEst(wolfboot, cerelaboot, type="Dhat4")
( BSmean <- mean(wolfcerela2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval
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[illegible]





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min(length(fox), length(capcap))
foxcapcapest<- overlapEst(fox, capcap, type="Dhat4")
foxcapcapest
overlapPlot(fox, capcap, main="Jul-Aug 2016-2018", rug = TRUE)
legend('topright', c("V. vulpes", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,70637", side=4)
Corner_text(text="nVULVUL:110 nCAPCAP:148",location= "topleft")

foxboot <- resample(fox, 10000)
dim(foxboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
foxcapcap2 <- bootEst(foxboot, capcapboot, type="Dhat4")
( BSmean <- mean(foxcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(foxcapcapest, foxcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.74387 (n=10000, 95% confidence interval [0.61090 ;0.79873])")

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table(majjun$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=majjun$Secondln * 2 * pi
#caution for changing the source file!

fox <- TimeRad[majjun$Species == 'VULVUL']
capcap <- TimeRad[majjun$Species == 'CAPCAP']
min(length(fox), length(capcap))
foxcapcapest<- overlapEst(fox, capcap, type="Dhat4")
foxcapcapest
overlapPlot(fox, capcap, main="May-Jun 2016-2018", rug = TRUE)
legend('topright', c("V. vulpes", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,74386", side=4)
Corner_text(text="nVULVUL:133 nCAPCAP:207",location= "topleft")

foxboot <- resample(fox, 10000)
dim(foxboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
foxcapcap2 <- bootEst(foxboot, capcapboot, type="Dhat4")
( BSmean <- mean(foxcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(foxcapcapest, foxcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.76687 (n=10000, 95% confidence interval [0.65878 ;0.82258])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(marcapr$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=marcapr$Secondln * 2 * pi
#caution for changing the source file!

fox <- TimeRad[marcapr$Species == 'VULVUL']
capcap <- TimeRad[marcapr$Species == 'CAPCAP']
min(length(fox), length(capcap))
foxcapcapest<- overlapEst(fox, capcap, type="Dhat4")
foxcapcapest
overlapPlot(fox, capcap, main="March-April 2016-2018", rug = TRUE)

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legend('topright', c("V. vulpes", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,88144", side=4)
Corner_text(text="nVULVUL:90 nCAPCAP:165",location= "topleft")

foxboot <- resample(fox, 10000)
dim(foxboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
foxcapcap2 <- bootEst(foxboot, capcapboot, type="Dhat4")
( BSmean <- mean(foxcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(foxcapcapest, foxcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.84064 (n=10000, 95% confidence interval [0.78972 ;0.95908])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(novfebrnew$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=novfebrnew$Secondln * 2 * pi
#caution for changing the source file!

fox <- TimeRad[novfebrnew$Species == 'VULVUL']
capcap <- TimeRad[novfebrnew$Species == 'CAPCAP']
min(length(fox), length(capcap))
foxcapcapest<- overlapEst(fox, capcap, type="Dhat4")
foxcapcapest
overlapPlot(fox, capcap, main="Winter 2016-2018", rug = TRUE)
legend('topright', c("V. vulpes", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,78832", side=4)
Corner_text(text="nVULVUL:174 nCAPCAP:124",location= "topleft")

foxboot <- resample(fox, 10000)
dim(foxboot)
capcapboot <- resample(capcap, 10000)
dim(capcapboot)
foxcapcap2 <- bootEst(foxboot, capcapboot, type="Dhat4")
( BSmean <- mean(foxcapcap2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(foxcapcapest, foxcapcap2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidence interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.80250 (n=10000, 95% confidence interval [0.69843 ;0.87297])")

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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table(szeptokt$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=szeptokt$Secondln * 2 * pi
#caution for changing the source file!

fox <- TimeRad[szeptokt$Species == 'VULVUL']
capcap <- TimeRad[szeptokt$Species == 'CAPCAP']
min(length(fox), length(capcap))
foxcapcapest<- overlapEst(fox, capcap, type="Dhat1")
foxcapcapest
overlapPlot(fox, capcap, main="Sept-Oct 2016-2018", rug = TRUE)
legend('topright', c("V. vulpes", "C. capreolus"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,78429", side=4)
Corner_text(text="nVULVUL:50 nCAPCAP:164",location= "topleft")

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[illegible]

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table(teljes161718$Species)

TimeRad=teljes161718$Secondln * 2 * pi
#caution for changing the source file!

cerelaplot <- TimeRad[teljes161718$Species == 'CERELA']
densityPlot(cerelaplot, rug=TRUE, adjust = 0.2)

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table(teljes161718$Species)

TimeRad=teljes161718$Secondln * 2 * pi
#caution for changing the source file!

susscrplot <- TimeRad[teljes161718$Species == 'SUSSCR']
densityPlot(susscrplot, rug=TRUE, adjust = 0.2)

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table(vulvull161718$Species)

TimeRad=vulvull161718$Secondln * 2 * pi
#caution for changing the source file!

vulvulplot <- TimeRad[vulvull161718$Species == 'VULVUL']
densityPlot(vulvulplot, rug=TRUE, adjust = 0.2)

#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEE
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#functional group analysis

table(total$Species)
#Dhat type depends on the number of observations of the smallest group in the comparison, <50
(type 1) or >75 (type 4)!

TimeRad=total$Secondln * 2 * pi
#caution for changing the source file!

wolf <- TimeRad[total$Species == 'CANLUP']
prey <- TimeRad[total$Species == 'PREY']
min(length(wolf), length(pre))
wolpreyest<- overlapEst(wolf, prey, type="Dhat4")
wolpreyest
overlapPlot(wolf, prey, main="Wolf and prey 2016-2018", rug = TRUE)
legend('bottomright', c("C. lupus", "Prey"), lty=c(1,2), col=c(1,4), bty='n')
mtext("Delta=0,87587", side=4)
Corner_text(text="nCANLUP:311 nPREY:2972",location= "top")

wolfboot <- resample(wolf, 10000)
dim(wolfboot)
preyboot <- resample(pre, 10000)
dim(preboot)
wolfprey2 <- bootEst(wolfboot, preyboot, type="Dhat4")
( BSmean <- mean(wolfboar2) )
#Difference between BSmean and Delta is the bootstrap bias, necessary for calculation of
Confidence interval

bootCI(wolboarest, wolfboar2)
#basic0 is the estimator that takes bootstrap bias into account
#overlap coefficient mean after bootstrapping: BSmean (n=10000, 95% confidance interval:
(basic0 lower; basic0 upper).
#at normal distribution, norm0 will be close to basic0

title(sub="BSmean=0.85560 (n=10000, 95% confidance interval [0.79851 ;0.97272])")

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## B) Random Encounter Model (R package: remBoot)

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library(help = "remBoot")

#packages required: remBoot, Rmisc, plyr, lattice

#calculating REM estimation density

#2016

CANLUP16 <- data.frame(CANLUP16_new)
head(CANLUP16)
tm <- 591
v <- 24.85
rem(CANLUP16, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
output <- remBoot(CANLUP16, tm, v, nboots, error_stat = c("ci"))
output
outputSD <- remBoot(CANLUP16, tm, v, nboots, error_stat = c("sd"))
outputSD

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#calculating REM estimation density
capcap16 <- data.frame(CAPCAP16)
head(capcap16)
tm <- 591
v <- 0.992
rem(capcap16, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(capcap16, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(capcap16, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot

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#calculating REM estimation density
cerela16 <- data.frame(CERELA16)
head(cerela16)
tm <- 591
v <- 1.984
rem(cerela16, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(cerela16, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(cerela16, tm, v, nboots, error_stat = c("sd"))
outputSD
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#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#calculating REM estimation density
boar16 <- data.frame(SUSSCR16)
head(boar16)
tm <- 591
v <- 5.763
rem(boar16, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(boar16, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(boar16, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#calculating REM estimation density
fox16 <- data.frame(VULVUL16)
head(fox16)
tm <- 591
v <- 7.88
rem(fox16, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(fox16, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(fox16, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#2017
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CANLUP <- data.frame(CANLUP)
head(CANLUP)
tm <- 793
v <- 24.85
rem(CANLUP, tm, v)
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#bootstrapping for calculation confidence interval
nboots <- 10000
output <- remBoot(CANLUP, tm, v, nboots, error_stat = c("ci"))
output
outputSD <- remBoot(CANLUP, tm, v, nboots, error_stat = c("sd"))
outputSD
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#calculating REM estimation density
capcap <- data.frame(CAPCAP)
head(capcap)
tm <- 793
v <- 0.992
rem(capcap, tm, v)
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#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(capcap, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(capcap, tm, v, nboots, error_stat = c("sd"))
outputSD
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#ggplot
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#calculating REM estimation density
cerela <- data.frame(CERELA_new)
head(cerela)
tm <- 793
v <- 1.984
rem(cerela, tm, v)
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```
#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(cerela, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(cerela, tm, v, nboots, error_stat = c("sd"))
outputSD
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#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#calculating REM estimation density
boar <- data.frame(SUSSCR)
head(boar)
tm <- 793
v <- 5.763
rem(boar, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(boar, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(boar, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#THEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTHEENDTH
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#calculating REM estimation density
fox <- data.frame(VULVUL)
head(fox)
tm <- 793
v <- 7.88
rem(fox, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(fox, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(fox, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#2018
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#calculating REM estimation density
CANLUP18 <- data.frame(CANLUP18)
head(CANLUP18)
tm <- 670
v <- 24.85
rem(CANLUP18, tm, v)
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```
#bootstrapping for calculation confidence interval
nboots <- 10000
output <- remBoot(CANLUP18, tm, v, nboots, error_stat = c("ci"))
output
outputSD <- remBoot(CANLUP18, tm, v, nboots, error_stat = c("sd"))
outputSD
```

```
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```
#calculating REM estimation density
capcap18 <- data.frame(CAPCAP18)
head(capcap18)
tm <- 670
v <- 0.992
rem(capcap18, tm, v)
```

```
#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(capcap18, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(capcap18, tm, v, nboots, error_stat = c("sd"))
outputSD
```

```
#ggplot
```

```
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```
#calculating REM estimation density
cerela18 <- data.frame(CERELA18)
head(cerela18)
tm <- 670
v <- 1.984
rem(cerela18, tm, v)
```

```
#bootstrapping for calculation confidence interval
nboots <- 10000
```

```

outputCI <- remBoot(cerela18, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(cerela18, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#calculating REM estimation density
boar18 <- data.frame(SUSSCR18)
head(boar18)
tm <- 670
v <- 5.763
rem(boar18, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(boar18, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(boar18, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +
  scale_x_continuous(name="Survey site") +
  scale_y_continuous(name="Animals.km2") +
  ggtitle("Animal density estimates calculated with REM and remBoot")

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#calculating REM estimation density
fox18 <- data.frame(VULVUL18)
head(fox18)
tm <- 670
v <- 7.88
rem(fox18, tm, v)

#bootstrapping for calculation confidence interval
nboots <- 10000
outputCI <- remBoot(fox18, tm, v, nboots, error_stat = c("ci"))
outputCI
outputSD <- remBoot(fox18, tm, v, nboots, error_stat = c("sd"))
outputSD

#ggplot
ggplot(rem, aes(x = site, y = rem$den)) +
  geom_bar(position = position_dodge(), stat="identity", fill="light blue") +
  geom_errorbar(aes(ymin=den-sd, ymax=den+sd)) +

```

```
scale_x_continuous(name="Survey site") +  
scale_y_continuous(name="Animals.km2") +  
ggtitle("Animal density estimates calculated with REM and remBoot")
```

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